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JOURNAL OF MAMMALOGY

Published Quarterly by the American Society of Mammalogists

VOL. 39 FEBRUARY 20, 1958 NO. 1

OBSERVATIONS ON FRESHWATER DOLPHINS IN THE UPPER AMAZON

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Although freshwater dolphins of the families Platanistidae and Delphinidae are among the more interesting and conspicuous members of the Amazon River fauna of South America, relatively little is known of their habits. The Amazon dolphin or bouto, *Inia geoffrensis* (Blainville), occurs throughout much of the Amazon and its principal affluents and in the Orinoco as well. River dolphins of the genus *Sotalia* also inhabit a considerable portion of the Amazon system, their range extending to over 1,600 miles above the mouth of the river.

In February, 1956, an expedition sponsored by Florida's Silver Springs was made to the upper Amazon at Leticia in the Commissary of Amazonas in southern Columbia to collect living freshwater dolphins for exhibition purposes. Both *Inia* and *Sotalia* were present in some numbers in the region visited, and four Amazon dolphins, which had been harpooned and captured alive, were obtained from natives and flown from Leticia to Florida. Of the four, one young female died en route and a young male succumbed shortly after arrival. The two surviving dolphins, both males, were kept at Silver Springs near Ocala, Florida.

As a member of this party, the writer had excellent opportunities to study *Inia* and *Sotalia* in their natural surroundings over a 15-day period from February 19 to March 2. Observations were largely confined to the environs of Leticia, although some data were obtained at the settlement of Ramon Castilho, Peru, directly across the river from Leticia, and in the vicinity of Benjamin Constant, Brazil (Fig. 1). The dolphins were watched daily for periods ranging from an hour or two to nearly the entire day. In addition, several night trips were made to investigate the extent of their nocturnal activity. The majority of observations were made from a 16-foot aluminum boat equipped with an outboard motor or from a small native canoe. The latter proved more satisfactory in that it was more easily and quietly maneuvered, thereby making it possible to approach the animals more closely without alarming them than with the larger craft. Occasionally the dolphins were viewed from vantage points on shore. In most instances the animals could be watched at distances near enough so that their activities were clearly discernible with the unaided

eye, but for observations at a distance or critical study at close range 6×30 binoculars were employed.

In September, 1956, Ross Allen, who led the first expedition, returned to the Leticia region for a period of three months. During this time he was able to make further observations on the habits of both dolphins and to obtain measurements and other data from 11 specimens that were captured. He has kindly made this additional information available for inclusion in the present report.

DESCRIPTION OF HABITATS

The major habitats in which dolphins were observed included the Amazon itself and the lower reaches of certain broad tributaries entering it, a series of three lakes connected to the

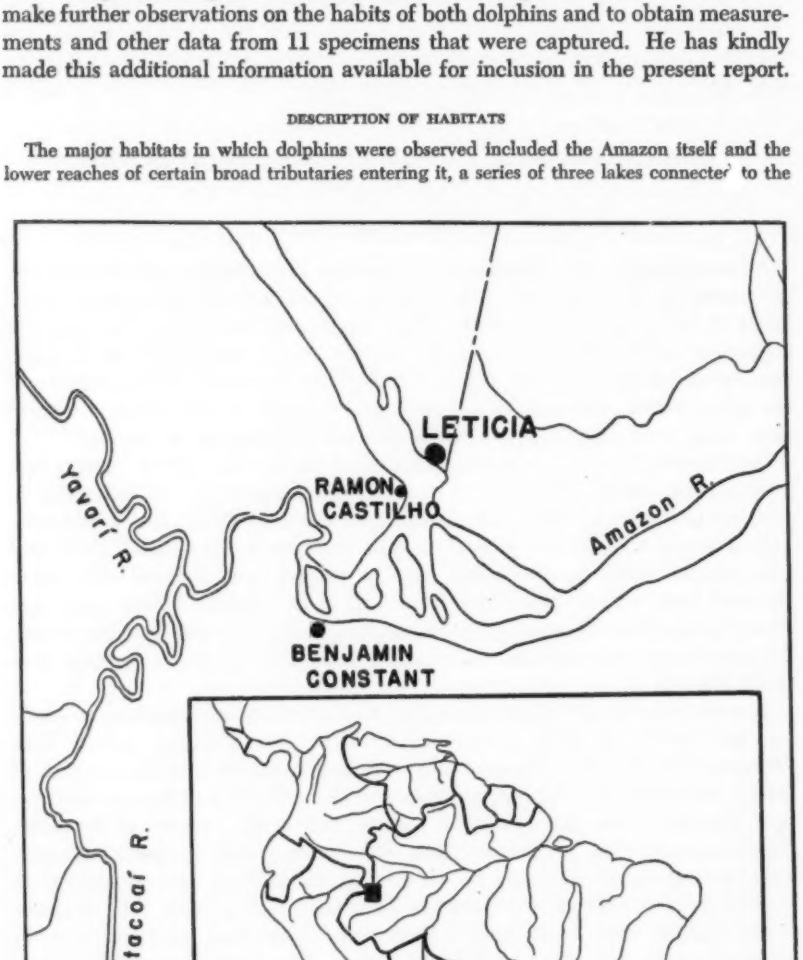

FIG. 1.—The region of the upper Amazon where observations on *Inia* and *Scotalia* were made and (insert) its location in northern South America.

Amazon by a narrow channel, and a small stream that entered the lake farthest removed from the main river.

Observations in February and March were made during the period of high and still rising waters in the upper Amazon. At this time the river in the vicinity of Leticia was some two miles wide, and its maximum current was estimated at between five and seven miles per hour. The flow was quite irregular, with quiet reaches alternating with stretches of eddies and upwelling. Branches, logs, entire trees, mats of hyacinth and other aquatic plants, and rafts of earth and vegetation torn from the banks were constantly being borne downstream. In some placid stretches, frequently in midriver, large quantities of such debris would occasionally be accumulated through eccentricities of the current. The water was brown and highly turbid. The surface temperature some distance from shore on March 2 was 80°F. Numerous large tributaries, smaller streams and lakes joined the main channel along its course to form a labyrinth of open waterways penetrating deep into the extensively flooded jungles bordering the river.

The lakes, where the dolphins were studied most intensively, were located approximately a mile north of Leticia. They lay in a somewhat stepwise order from east to west and with their long axes more or less paralleling the Amazon. They ranged in size from about one to two miles long and from one-fourth to one-half mile wide. Their combined surface area was estimated at roughly five square miles. The channel connecting them with the river originated at the south end of the first lake and was about 500 yards long and 40 to 50 yards wide. With the rise of water levels, the lakes had overflowed their banks and inundated the surrounding forests, the normal boundaries between their basins being marked only by strips of jungle flooded to a considerable depth. A narrow, short channel of open water joined the first and second lakes, while a broader gap of open water existed between the middle and last. A single sounding in the channel between the first two lakes gave a depth of 26 feet, and it is probable that maximum depths in the lakes well exceeded this figure. There was no appreciable movement of water between the lakes and river, and the former were noticeably less turbid than the latter. A surface temperature of 86°F. was recorded in the lakes on March 2, although deeper waters felt appreciably cooler. It is probable that surface temperatures in the lakes more closely approximated air temperatures and averaged warmer than in the main river. This may have been a factor influencing the activity of dolphins in the lakes under certain weather conditions or at different times of the year.

The small stream that emptied into the southern end of the third lake meandered in a northerly direction for several miles above the lake. For a mile or so beyond its mouth it averaged 20 or so yards wide and was apparently over 20 feet deep. It was bordered on one side by flooded jungle and on the other by higher ground, some of which had been partially cleared for agricultural purposes or Indian village sites. The water of the stream exhibited about the same degree of turbidity as that of the lakes. Since the stream was well shaded along its course, surface temperatures probably averaged somewhat lower than in the lakes. A temperature of 84°F. was obtained on March 2 at about noon and within a few minutes of the time other readings were taken in the Amazon itself and lakes. There was only a very slight current evident in the stream.

According to residents in the area, the lakes and stream were subject to drastic seasonal fluctuations. Upon the subsidence of the water in late spring and summer, the depth of the lakes is said to drop to about four to six feet and their surface area to diminish to nearly one-fifth the wet season maximum. The channel leading to the main river eventually becomes dry, or nearly so, with the result that the lakes are essentially isolated from the Amazon for a part of the year. The stream draining into the last lake is reduced to a mere trickle scarcely knee-deep.

Inia and *Sotalia*, both locally called "bufeo," were frequently observed in the Amazon and in the larger tributaries investigated. It appeared that in the main river the dolphins preferred the quieter and probably shallower waters near the edge rather than the swifter parts toward the center of the river. Individuals seen were invariably within a few hundred yards, often

50 to 100, of the shore, despite the fact that a sharp lookout was kept for dolphins in midstream on the several occasions that trips were made across the river. Both forms were most frequently noted in coves, along shorelines bordered with stands of emergent aquatic vegetation, or off the mouths of streams entering the river, and it might be supposed that they were attracted to such situations by an abundance of fish.

Both dolphins also frequented the lakes, where they seemed to prefer open water. Although they were often seen skirting the edge of the bordering forest, they apparently seldom entered it. Boutos were noted within the flooded jungles on only three occasions, and then only a few yards from open water, while river dolphins were never recorded there. However, that both do at times penetrate deep into inundated forests is indicated by observations made by von Humboldt and Bonpland (1852) and Sanderson (1956). The dolphins roamed freely throughout the three lakes and were as numerous in the last as in the two nearer the Amazon. Individuals of both species were frequently seen entering or leaving the lakes through the channel. The extent of the movements suggests that few, if any, individuals of either resided entirely in the lakes throughout the season of high water.

Although inias were occasionally noted near the mouth of the stream in the third lake, only *Sotalia* was known to actually enter it. A single individual, perhaps the same animal each time, was seen in the stream over one-half mile above the lake a number of times. It was always swimming steadily up or downstream when seen, appearing never to loiter in any particular stretch.

Local inhabitants reported that dolphins were present in the lakes and stream only during the period of high waters and that they returned to the Amazon sometime prior to the time when the lakes became finally cut off from the river by the decline in water level. Bates (1864) described in detail the variations of the seasons in the upper Amazon and pointed out that turtles and other aquatic animals tend to leave the river for the shallower waters of the flooded lands when waters rise and that there is a marked reverse migration upon their recession. The egress of the dolphins from the lakes and stream during the dry months may thus be at least partly the result of a similar exodus by their food fishes, although the shallowness and high temperature of the water in those habitats at that time of the year may also be important factors.

NUMBERS

Based upon the frequency with which individuals were seen in all habitats combined, *Inia* outnumbered *Sotalia* in the proportion of about 2:1 in the region of Leticia. The former were most abundant in the lakes, a rough census performed on February 27 affording some idea of the magnitude of the population there at a given time. In the early afternoon on this date the three lakes were carefully surveyed, working from the last to the one nearest the Amazon, in an attempt to determine as nearly as possible the number of dolphins present. A total of 14 *Inia* were counted. This figure was probably quite close to the actual number in the lakes at that time even though the possibilities of overlooking some individuals or duplicating counts are taken into account. Following this, a position was taken on a log raft moored at the entrance of the channel in order to enumerate the number of dolphins entering or leaving the lakes before darkness. In the time from 4:00 to 5:30 PM, 11 *Inia* and 3 *Sotalia* passed by on their way into the lakes from the Amazon. No movement was noted in the opposite direction. Thus by late afternoon there were approximately 20 to 25 *Inia* in the lakes, a density corresponding to around 4 or 5 animals per square mile of water. This estimate can probably be considered near the maximum number of Amazon dolphins to be found in the lakes at any one period, since greatest dolphin activity there occurred in the early morning and late afternoon when more animals appeared to be present than at other times of the day.

Three was the greatest number of river dolphins counted in the lakes during any one period. Too little time was spent on the main river to permit even a crude estimate of the density

of either Amazon or river dolphins in that habitat. However, no concentrations of *Inia* approaching the densities observed in the lakes were encountered in the Amazon. On the other hand, more *Sotalia* were seen in the main river than in the lakes and stream. It is possible that these observations may indicate differences in habitat preference between the two forms, but they are insufficient to be conclusive.

PHYSICAL CHARACTERISTICS

The thickset body, long low dorsal fin, conspicuous melon, greatly produced jaws, tiny eyes and relatively large pectoral fins are among the principal external characteristics of the Amazon dolphin (Plate I). Individuals seen in the field were judged to range from about 4 to 8 or 9 feet in total length, with the majority averaging about 5 or 6 feet. Body measurements of the two partly grown *Inia* that died and were presented to the University of Florida mammal collection by Florida's Silver Springs are given in Table 1. The female weighed 80 lbs., the male, 81. During his second sojourn at Leticia, Allen had the opportunity of measuring ten *Inia* that were collected in the vicinity. An individual of unknown sex had a length of 9 feet. Six males measured 4½, 6, 7, 8, 8 and 9 feet, while the total lengths of three females were 6, 6 and 8 feet. The largest of the females, captured December 7, was reported to be lactating.

Measurements of the skulls of three of the specimens examined by Allen are given in Table 2. Unfortunately a record was not kept as to the sexes and lengths of the individuals from which the skulls were obtained. Skull 1 is undoubtedly from a young animal, as indicated not only by its small size but also by the fact that the teeth are unworn and have

TABLE 1.—*Measurements of two partly grown specimens of Inia geoffrensis from the upper Amazon in the vicinity of Leticia, Colombia*

MEASUREMENTS, mm.	MALE	FEMALE
Length from tip of beak to base of median notch in posterior margin of flukes	1626	1562
Length of head from occipital crest to tip of beak	464	432
Greatest breadth of head	190	183
Length of beak from transverse groove in front of melon to tip	203	213
Width of beak at base	73	67
Depth of beak at base	79	73
Width of beak at tip	24	32
Depth of beak at tip	38	38
Greatest length of fleshy orbit	10	8
Greatest height of fleshy orbit	4	5
Distance from anterior margin of orbit to tip of beak	283	292
Greatest width of flukes when normally expanded	483	419
Length of flipper	318	292
Greatest width of flipper	172	151
Greatest height of dorsal fin	64	67
Greatest depth of caudal peduncle	151	140
Greatest width of caudal peduncle	59	57
Greatest width of closed blowhole	37	38
Greatest circumference of head	632	635
Circumference of body at posterior base of pectoral fin	708	737
Width of body between bases of pectoral fins	89	114

roots which are truncated and widely open, so that the pulp cavity is in broad communication with the exterior. Skull 2 is apparently that of an older individual. The roots of the teeth are completely closed and tapering. The crowns are generally unworn, except in the case of a few posterior teeth on the left side that do show slight wear. This condition may be somewhat aberrant, as the jaws of this specimen are slightly twisted. The roots of the teeth of skull 3 are closed and many of the teeth show wear both on the tips and sides. This,

TABLE 2.—*Skull measurements of Inia geoffrensis*

MEASUREMENTS, mm.	SPECIMEN NO.		
	1*	2	3†
Total length (from most posterior bulge of braincase to tip of rostrum)	425(?)	469	510
Height from vertex to level of ventrolateral processes of occipital	155	166	167
Breadth across squamosal processes (greatest breadth)	180	199	210
Least interorbital breadth	112	125	122
Length from most posterior bulge of braincase to line connecting bases of antorbital notches	155	160	168
Length of rostrum from a line connecting bases of antorbital notches to tip	274(?)	314	347
Breadth of rostrum at base	76	84	82
Breadth of rostrum at midlength	29	30	30
Breadth of rostrum at level of 3rd tooth from tip	23	23	21
Greatest length of right premaxillary	360(?)	403	443
Greatest length of left premaxillary	359(?)	404	444
Maximum breadth of premaxillaries at anterior margin of anterior nares	54	59	57
Breadth of premaxillaries at mid-rostral length	20	23	21
Length of maxillary tooth row	242(?)	264	305
Breadth of anterior nares	24	28	26
Maximum breadth of foramen magnum	32	32	
Maximum height of foramen magnum	32	36	
Greatest breadth across occipital condyles	73	73	
Greatest breadth of right condyle	23	26	
Greatest breadth of left condyle	25	27	
Maximum length of right condyle	40	42	
Maximum length of left condyle	40	41	
Length of mandible (straight line)	—	413	448
Distance from apex of coronoid process to apex of angle of mandible	81	93	101
Height of mandible at beginning of symphysis	22	26	27
Length of symphysis	—	222	234
Length of mandibular tooth row	—	270	306

* Tip of rostrum damaged and distal extremity of mandibles broken off.
† Occipital condyles and portion of occipital bone surrounding foramen magnum missing.

together with its greater size, suggests that this skull is from an older individual than either 1 or 2. Certain dental anomalies exist in the two larger skulls. The most posterior tooth in the right maxillary row of skull 2 is much reduced and peglike. Although apparently not functional, it possesses a well-formed root and a crown that is sculptured into irregular sharp crests, which bear no resemblance to the conformation of the normal corresponding tooth on the left side. In the larger skull, the first tooth of the right maxillary is rudimentary, its alveolus being only about half the size of the initial one on the left. In addition, a partially formed socket is evident at the posterior end of the left maxillary tooth row. This probably marks the site at which a tooth failed to develop, as a normal tooth occupies the same locus on the opposite side. A gap of about 23 mm. also exists between the last two alveoli and the remainder of the dental row in the right dentary of this specimen. Two shallow depressions are visible in the bone in this space and appear to represent incomplete alveoli in which no teeth were present. Two distinct sockets occupy the same position in the left ramus.

The number of normal teeth or definitive alveoli in specimens 2 and 3 are R 24/25 + L 26/26 = 101 and R 26/25 + L 26/28 = 105, respectively. Because of the damaged distal portion of the rostrum and mandibles of skull 1, its tooth count cannot be accurately determined, although the number is estimated as R 25/24 + L 25/24 = 98. The total numbers of teeth for ten specimens of *Inia* cited by Ribeiro (1943) range from 104 to 132, with an average of 113.

The rather wide color variation that exists in Amazon dolphins is one of the best known characteristics of the species. In this regard, Beddard (1902) remarked that "Its colour variations are rather extraordinary, unless they can be set down to sex, which has been denied. Some individuals are wholly pink; others are black above and pink beneath." Ribeiro (1943) has postulated that this marked degree of color variation in *Inia* is due to age, the animals presumably being dark at birth and becoming progressively paler as they grow older. An equally well-marked sequence of color changes correlated with age classes has been described for the beluga, *Delphinapterus leucas* (Vladykov, 1944). In this species the lightening with age was demonstrated to be due to the diminution of melanic pigment in the epidermis.

The present observations are in accord with Ribeiro's interpretation. Of the four specimens of *Inia* captured and flown to Silver Springs, the smallest had dark, grayish-black upperparts that gradually shaded into lighter gray beneath. There was no distinct line of demarcation between the dorsal and ventral colors as has sometimes been indicated in figures of *Inia*. The male that died was slightly larger than the female and was somewhat lighter gray above and below. While still alive the dolphin showed a pinkish hue on the ventral portions of the body, but this color faded shortly after death. The smaller of the two dolphins surviving the flight was somewhat larger than the individual last mentioned, which it closely matched in coloration, including the existence of the pinkish tint on the lower parts of the body. The largest of the four measured approximately 7 feet in length. It possessed very light upperparts of a dusky-gray that tended to be concentrated in irregular blotches along the middorsum and upper sides. This dark pigment was heaviest around the blowhole and on the summit of the head. The entire body was suffused with pinkish, although the color was particularly conspicuous on the venter and lower sides and along the leading edge of the dorsal fin. Thus even in this small series of individuals a correlation between size and coloration is evident.

Field observations provide further evidence of this relationship. The smallest *Inia* seen were dark slate-gray above and slightly lighter below. Animals of somewhat greater size, approximately 5 or 6 feet, were noticeably lighter, and the skin had taken on a pinkish tint that was most apparent on the lower sides and belly. The largest individuals observed were quite pale and strikingly flesh-colored or pinkish, a characteristic alluded to in one of the Portuguese common names for the beasts—"boto vermelho." As in the largest captive, the light dusky or bluish-gray pigmentation in these adults appeared to be largely restricted to

the middorsum in a faint blotchy pattern. The dark pigment was also more pronounced on the top of the head in the vicinity of the blowhole than elsewhere on the body in several large specimens viewed at close range. It is possible that the concentration or persistence of pigment in this region is of functional significance to the animals by preventing sunburn of that portion of the body regularly exposed above the surface for relatively long periods in the action of breathing. In view of the apparent effect of increased light on the pigmentation

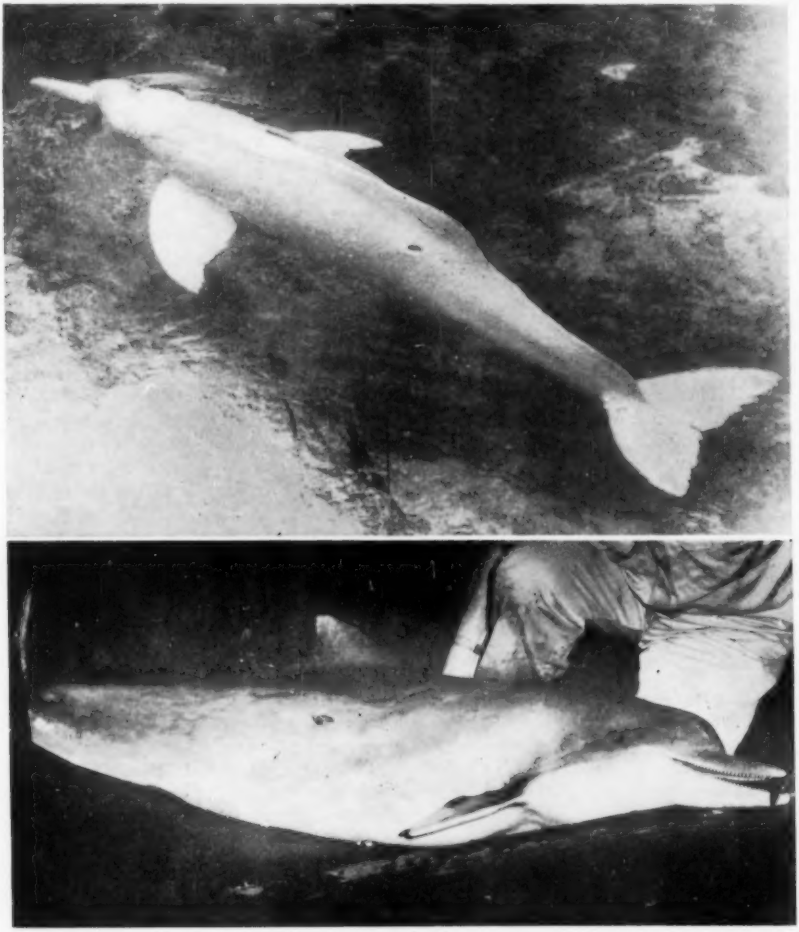

PLATE I

ABOVE: A captive adult male *Inia geoffrensis* photographed at Florida's Silver Springs. The dolphin is shown surfacing to breathe in the typical manner. The dark spot below the dorsal fin is a partly healed harpoon wound. BELOW: A male *Sotalia* collected about 12 miles above Leticia on December 4, 1956 (from a Kodachrome by Mrs. E. Ross Allen). Highlights obscure some details of the color pattern mentioned in the text.

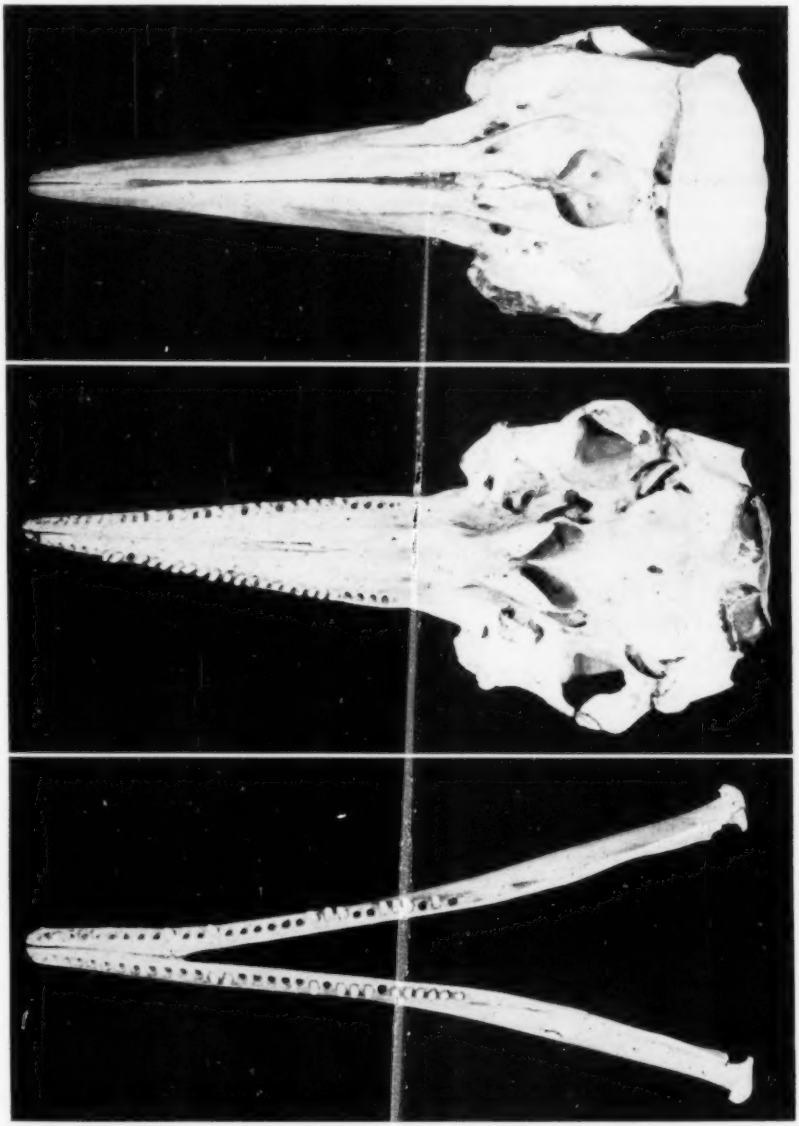

PLATE II

Views of the skull of *Sotalia*. UPPER: Dorsal aspect. MIDDLE: Ventral aspect. LOWER: Mandibles from above.

of captive *Inia* mentioned beyond, it is possible that the more intense pigmentation in this area reflects a response of the epidermis to frequent exposure to sunlight. The pinkish hue, which appears to become increasingly more apparent with the fading of the dark coloration in larger individuals, is apparently due to blood in vessels in or beneath the skin.

It is of interest to note, with respect to the color variation in this species, that the two captive specimens which were kept in extremely clear and fairly shallow water exhibited a gradual darkening of the body over a six-month period. This suggests that the color changes seemingly undergone during growth are not entirely irreversible and may be influenced to a certain extent by local environmental factors, particularly the clarity of the water. A statement appearing in an account of *Inia* by Kellogg (1940) to the effect that boutos in the large rivers vary from bluish-gray to flesh-colored above, while those entering the larger lakes during high waters tend to be blackish, may be explainable on this basis if it be assumed that such lakes are less turbid than the main rivers at this time of the year, which is probably true, and that the *Inia* population is entirely or nearly restricted to these waters. Given such conditions, the animals might become darker over a period of several months through the maintenance or redevelopment of dark pigment in response to greater light penetration. There were no such differences evident between the inias seen in the lakes and main river during the course of the present study, perhaps because the animals ranged freely back and forth between the two habitats.

River dolphins are much more typically porpoiselike in their appearance and actions than *Inia*. They were distinguishable from the latter at some distance by their prominent dorsal fin. Their beak, though well developed, is more abbreviated than that of *Inia*, and the forehead does not bulge so prominently as to markedly interrupt the streamlined contour of the head. Individuals observed in the field were estimated to vary from about 3 to 5 feet in total length and to average about 4. A single specimen (Plate I) that was harpooned by a native in the Amazon approximately 12 miles above Leticia on December 4 was measured by Ross Allen and Marlin Perkins with a cloth tape. The following measurements were recorded: total length from base of notch in flukes to tip of beak over the curve of the body, 61¼; distance from tip of beak to blowhole, 12; distance from notch of flukes to tip of dorsal fin, 29; greatest girth, 35; spread of flukes, 17; greatest width of flukes, 5½; height of dorsal fin, 5; length of mouth, 9½; greatest length of flipper, 8½; and greatest width of flipper, 4¼ in. The skull of this individual was saved (Plate II) and its measurements are presented in Table 3.

On the basis of Allen's notes and a color transparency, the animal was bluish or pearl gray above, the color being darker on the anterior part of the body. The upper and lower surfaces of the flippers were of the same color as the dorsum. The leading edge of the fin was slightly darker than the rear part. The lower jaw and throat were pinkish-white and the belly, white. From the photograph it can been seen that the dark upperparts and light venter meet anteriorly at a distinct line extending from the corner of the mouth to the base of the pectoral fin. The eye lies above this line in the dorsal coloration. Behind the flipper a well-defined band of ventral color extends dorsad to slightly above the level of the eye. Beyond this light band the dorsal coloration extends progressively farther down on the side in a smooth curve until it appears to reach the midventral line just behind the anus. The demarcation between the darker upperparts and lighter venter is less sharply defined posterior to the pectoral fin than anteriorly. The tip of the beak and apex of the dorsal fin appear whitish.

Details of coloration and pattern in *Sotalia* were difficult to observe in the field because these dolphins moved about rather rapidly and appeared only momentarily when rolling. The smaller specimens seen were dark gray, almost black, above and light pinkish below. The two colors were clearly separated along the sides. Although the coloration of the flippers and the presence or absence of a white band behind them were not noted, three individuals viewed at unusually close range on one occasion showed conspicuous whitish

blotches on the tip of the beak and dorsal fin similar to those visible in the photograph of the specimen collected. The largest *Sotalia* observed were noticeably paler above than the smaller individuals.

The specific identity of the river dolphins in the Leticia region is uncertain, as the taxonomy of the genus in the Amazon River system as a whole is presently poorly understood. Although three species, *Sotalia fluviatilis* (Gervais), *S. pallida* (Gervais) and *S. tucuxi* (Gray), have been described from the Amazon, their validity is highly questionable. True (1889) summarized the information available to that time which pertained to these species and was unable to arrive at any satisfactory conclusion regarding their status on the basis of the fragmentary nature of the descriptions and great scarcity of suitable skeletal material. More recent references to any of these species fail to provide any further clarification of their relationships. For example, Cabrera and Yepes (1940) list *Sotalia pallida* as the sole fluviatile representative of the genus in South America, Vieira (1955) includes *Steno* (= *Sotalia*) *tucuxi* in the synonomy of *pallida*, while Carvahlo (1955) refers to river dolphins seen near Benjamin Constant, Brazil, as *Sotalia tucuxi*. At the same time, none of these authors indicates the basis of selection for the particular binomial employed.

TABLE 3.—*Skull dimensions of a male Sotalia from the Amazon River in the vicinity of Leticia, Colombia*

MEASUREMENTS	mm.
Condylobasal length	363
Height from frontal tuberosites to inferior border of pterygoids	120
Breadth across squamosal processes (greatest breadth)	155
Breadth across middle of orbits	129
Length from occipital condyles to line connecting bases of antorbital notches	149
Length of rostrum (from a line connecting bases of antorbital notches to tip)	220
Breadth of rostrum at base	70
Breadth of rostrum at midlength	39
Breadth of rostrum at level of 3rd tooth from tip	15
Greatest length of right premaxillary	294
Greatest length of left premaxillary	281
Maximum breadth of premaxillaries at anterior margin of anterior nares	56
Breadth of premaxillaries at mid-rostral length	22
Distance from anterior end of premaxillaries to posterior margin of pterygoids	267
Length of maxillary tooth row	189
Breadth of anterior nares	37
Maximum breadth of foramen magnum	39*
Maximum height of foramen magnum	34
Greatest breadth across occipital condyles	79
Greatest breadth of right condyle	24
Greatest breadth of left condyle	23
Maximum length of right condyle	46
Maximum length of left condyle	44
Length of mandible (straight line)	311
Height of mandible at coronoid process	70
Height of mandible at beginning of symphysis	17
Length of symphysis	67
Length of mandibular tooth row	185

* Small portion of edge of foramen missing.

The impression gained from the field work in the vicinity of Leticia was that only a single form of *Sotalia* existed there, the differences in size and coloration noted appearing to be within the range of individual and age variation that might normally be expected within a single species population. Admittedly the evidence for this assumption is hardly conclusive, considering the difficulty of making critical observations on details of coloration and structure of such animals in the wild. However, this interpretation is supported by the fact that there seemed to be no obvious behavioral differences between individuals differing in size and color nor any tendency toward segregation of dolphins into groups of similar appearance, as might be expected if more than a single species were involved.

The specimen collected by Ross Allen cannot definitely be assigned to any of the Amazonian species of *Sotalia* on the basis of comparison with the original diagnoses of *fluviatilis* and *pallida* by Gervais (in Castelnau, 1855) and the scanty data assembled for *tucuxi* by True (1889). It agrees with *fluviatilis* and *tucuxi* in having dark upperparts and whitish underparts, as contrasted with *pallida*, which is described as being pale yellowish-white dorsally and white below. If the descriptions of the dorsal coloration of the specimens upon which *fluviatilis* and *tucuxi* are based are taken literally, the Leticia example may be somewhat lighter above than either of the others. Further particulars of color pattern and shape and proportion of the fins are available only for *fluviatilis* and *pallida*. In possessing pectorals of the same color as the dorsum and a prominent band of ventral color extending upwards on the sides of the body behind these fins, the Leticia specimen agrees quite closely with both the description and figure of *fluviatilis*. The flippers are of the same color as the ventral surface in *pallida* and are situated below the line of contact between the dorsal and ventral coloration, the separation being more regular than in *fluviatilis*. The Leticia specimen also more closely resembles *fluviatilis* in the shape of the dorsal fin but falls somewhat intermediate between the latter and *pallida* in the shape and relative size of the pectoral fins. The flippers of *fluviatilis* are relatively long. As taken from the figure in Castelnau, their length is contained approximately 1.5 times in the distance from the anterior margin of the base of the flipper to the tip of the rostrum. In the figure of *pallida* this proportion is about 2.3, while the value for the Leticia male, based on actual measurements, is 2.0.

Other than reflecting size differences between the specimens involved, the body measurements available for *fluviatilis* and *pallida* are of little worth as indications of specific differences. The total length and greatest girth of the type of *fluviatilis* are 1100 and 700 mm., respectively, and 1650 and 980 mm., for *pallida*. Thus the Leticia specimen is intermediate in size between the two. The skull dimensions of these specimens indicate a similar size relationship. Two skulls of the types of *tucuxi* were noted by True (1889) as being from immature animals, which, as judged from rostral length and total length of skull, were smaller than the type of *fluviatilis*. The number of teeth possessed by the Leticia specimen is 32/31, as compared with 28/27 or 29/28 given for *fluviatilis*, 30/31 for *pallida*, and 30/30 for *tucuxi*. In view of the rather marked variability in number of teeth within the same species of some toothed whales, these few counts do not seem to differ significantly.

A review of the descriptive material available for the three species of Amazon river dolphins strongly suggests that the principal characteristics employed to separate them may with equal justification be interpreted as being merely age differences of but a single species. On this basis, the variation encountered in the color of the upperparts would be considered as the result of a progressive loss of pigment with increasing age, as in the case of certain other cetaceans. The specimens discussed above nicely fit this hypothesis, since both with respect to increasing size and increasing paleness of upperparts, they rank in the same order, i.e., *tucuxi*, *fluviatilis*, Leticia specimen and *pallida*. Field data also suggest such a relationship. The apparently marked dissimilarity of the actual color pattern of *fluviatilis* and the Leticia specimen to that of *pallida* is perhaps less easily discounted as being simply an age variation, but such may indeed be the case. It is possible that the depigmentation accompanying growth may progress from the lower sides dorsally, so that in older specimens the line of juncture

between the dorsal and ventral colors may lie higher on the sides than in young animals. Thus the pectorals may be initially of the same color as the dorsum but grow lighter along with the lower sides as growth ensues and eventually come to be situated entirely within the ventral coloration. The *fluviatilis* and Leticia specimens might consequently represent intermediate stages in this transition where the pectorals, although still dark, are in the process of becoming isolated from the dorsal coloration by the reduction of pigment along the sides of the body. The light band behind the flippers might be explained on the basis that the rate of disappearance of the dark pigment is more rapid at some points along the body than at others.

The differences in the shape and proportions of the dorsal and pectoral fins between *fluviatilis, pallida* and the Leticia example might also be easily attributed to ontogenetic changes, the dorsal fin becoming relatively lower with age and the pectorals relatively shorter. Such a correlation between size and fin conformation does appear to exist in the material for which adequate data pertaining to these aspects are available.

A *Sotalia* measuring 51 inches collected near the mouth of the Rio Negro and examined by Natterer is described as having dark gray upperparts, with the pectorals of the same coloration (von Pelzeln, 1883). According to the measurements given, the pectorals are approximately of the same relative size as those of *fluviatilis,* which it most closely approaches in size. Thus, on the basis of size, at least the coloration and proportion of the flippers of this specimen agree closely to what would be predicted on the assumption that the traits under consideration vary with age in the manner suggested. Despite the fact that the scanty data at hand appear to favor the conclusion that the three nominal species of *Sotalia* in the Amazon are in actuality merely age variations of a single form, it is obvious that their taxonomic status cannot be satisfactorily resolved without a thorough revisionary study based upon adequate material from throughout the range of the genus in South America. Consequently, for the purposes of the present paper, it has seemed advisable to avoid the use of a specific trivial for the *Sotalia* of the Leticia region.

SWIMMING AND BREATHING

Amazon dolphins typically swam at a leisurely pace averaging about 2 m.p.h. It appeared that the dolphins did not go very deep between breaths, for in several instances individuals that were startled some time after they had disappeared following a breath roiled the surface in leaving the scene, indicating that they had remained within several feet of the surface after submerging.

When swimming slowly, the dolphins came to the surface to breathe in a horizontal position (Plate I). The top of the head was nearly always the first part of the body to appear, although on rare occasions the beak broke the surface first. Ordinarily the head was not sufficiently exposed to bring the eyes above water, and often the upper part of the melon and area surrounding the blowhole were the only portions of the body visible during the entire breathing cycle. Frequently, though, the dorsal fin and ridge of the back would rise gently out of the water after the head had appeared and shortly before the dolphin slipped quietly back beneath the surface. When surfacing in this manner, the animals ordinarily behaved in a languid manner, although under some conditions the action was much more quickly performed.

Usually the only sounds accompanying the surfacing were faint gasps associated with exhalation and inhalation. At other times the air was released with a sharp, explosive blowing sound, which was occasionally accompanied by a prominent, inverted pear-shaped spout that arose perpendicularly some 6 or 8 feet into the air. The spray was visible only momentarily before dissipating. As an example of the infrequence of spouting an instance may be cited in which a band of four or five inias was being watched and only a single spout was seen during the more than 30 surfacings observed. Rarely, a stentorian, sneeze-like snort was emitted by dolphins at the surface, apparently for the purpose of clearing the nasal passages of water or mucus.

The times of 19 intervals between surfacings were recorded for ten individuals swimming at normal speeds. The periods between breaths ranged from 5 to 112 seconds, with an average of 32 seconds. In all cases the blowhole remained above water for several seconds, but the actual time it stayed open could not be definitely ascertained. Several individuals that were kept under continual surveillance for some time were noted to come to the surface for air at rather short intervals for several consecutive times and then remain submerged for a period of longer duration.

One observation was made which indicated that the animals occasionally expelled a considerable volume of air when at some distance below the surface. In this case, a large inia being watched from a boat submerged following a breath and swam toward the boat. As it passed beneath, too deep to be visible, its course was marked by a string of large bubbles that came to the surface. The dolphin did not reappear for a breath on the other side of the boat until some moments later, at which time a typical horizontal surfacing occurred.

The significance of this phenomenon is unclear. It may have been either an aberrant variation of the normal breathing cycle or an act involving some sort of vocalization, as bubbles are known to issue from the blowhole when certain high-pitched whistling notes are uttered by several species of odontocetes (Kritzler, 1952). However, the volume of air released in this instance apparently much exceeded that ordinarily escaping when such calls are given, although this does not preclude the possibility that some other kind of sound was being produced.

At times *Inia* were seen to execute rolls in more typical porpoise fashion. In the most frequently observed type of roll, which appeared to be associated with feeding activity, the body was arched high out of the water and the dolphin seemed to pitch forward as it dropped back beneath the surface. The steep angle at which the animal entered the water gave the impression that it was sounding. The flukes did not usually appear above the surface. In some instances, the head appeared first, as in an ordinary horizontal surfacing, and a breath would be taken. Then the head would dip back beneath the water and the jackknifed trunk rise into view. A loud blow sometimes accompanied this performance. The roll was often accomplished more rapidly, the head and trunk making a continuous arc. Then only a hurried puff was heard, and the blowhole was exposed for merely a fraction of the time it was during the typical surfacing. After a series of such fast rolls, inias were sometimes seen to come to the surface and "glide" breathe at frequent intervals, as if replenishing their oxygen supply and resting from the more strenuous activity.

In spite of their generally somewhat lethargic behavior, inias were capable of considerably greater activity when the situation demanded. Several times individuals in the lakes were seen to swim swiftly from open water to the edge of, or actually into, the bordering flooded forests. They were also frequently observed swimming through the channel connecting the lakes to the Amazon at speeds four or five times greater than the usual cruising rate. At such times they appeared to swim fairly close to the surface, and their progress was marked by a prominent V-shaped wave and boiling wake. Such bursts of speed seldom lasted for more than 100 yards. When swimming rapidly the dolphins rolled to breathe. The form of the roll was much different from that believed to have been connected with feeding in that it was always rapidly executed and the body cleaved the water in a low arc instead of rising conspicuously above the surface.

Sotalia gave the impression of being considerably more active animals than *Inia*. They habitually swam at a faster pace than did the Amazon dolphins and, whereas the latter frequently seemed to swim aimlessly about, *Sotalia* invariably appeared to be following some purposive course. Perhaps because of their consistently greater momentum, river dolphins always rolled out of the water when breathing. The roll was somewhat similar to that of a fast-traveling *Inia* but much different from the more usual roll of the latter in that the back was not elevated so high out of the water nor did the animal give the impression of toppling forward when submerging. The entire cycle was always rapid, taking less than two

or three seconds. The head and trunk normally appeared in a smooth, uninterrupted sequence, although infrequently a slight hesitation between the time the head was thrust out and the body followed was evident. The flukes occasionally appeared during a roll when an animal was swimming rapidly near the surface or breasting the current in the Amazon. A short puff was the only sound heard during breathing. A small spout of water several inches high was noted in several instances as dolphins rolled to breathe, indicating that exhalation had begun before the blowhole had cleared the water. The intervals between breaths of six *Sotalia* that were timed were not greatly different from *Inia*, varying from 5 to 85 seconds and with a mean of 33 seconds.

The account by Bates (1864) of respiratory behavior of *Inia* and *Sotalia tucuxi* in the lower Amazon is difficult to reconcile with the present observations. With regard to the Amazon dolphin, he stated that "the top of the head is the part first seen; it then blows, and immediately afterwards dips head downwards, its back curving over, exposing successively the whole dorsal ridge with its fin. It seems thus to pitch heels over head, but does not show the tail fin." This description seems clearly to apply to the type of roll here considered to be characteristic of feeding behavior, but no mention is made of the low-arched roll executed when the dolphins are swimming rapidly nor the more commonly seen horizontal surfacing. Referring to *Sotalia*, Bates noted that ". . . it rises horizontally, showing first its back fin; draws an inspiration, and then dives gently down, head foremost." In only one case was Sotalia in the Leticia area seen to surface in this manner, and this appeared to be due to circumstances connected with feeding. Except for the statement that the back fin appears first, the description could well be of the horizontal method of breathing commonly employed by *Inia*. It is possible that either *Sotalia* in the lower reaches of the Amazon characteristically surfaces in the manner indicated by Bates, a fact which might be of taxonomic significance, or that he was perhaps unaware of the variability in the breathing behavior of *Inia* and mistakenly attributed instances of horizontal or "glide" breathing to *Sotalia*.

Several other variations of swimming behavior were noted. Both dolphins were seen to leap completely out of the water to heights of as much as 4 feet on several occasions. Only large individuals of *Inia* were observed to perform in this manner, and the cause is not clear. Amazon and river dolphins also exhibited positive rheotropism when swimming in a current. Individuals in the Amazon just off the mouth of the channel were often watched for periods of 15 minutes or longer as they breasted the current, surfacing time after time at about the same spot or forging slowly ahead. A similar tendency would seem to be indicated by certain behavior of a captive pilot whale, *Globicephala*, described by Kritzler (1952). During feeding this animal was noted to swim clockwise in a tank with a counter-clockwise circulation and at other times to thrust its snout into the stream of water issuing from intake jets in the bottom of the tank, as if in enjoyment of the flow of current over its body. In one instance a member of the party discovered a large *Inia* floating quite motionless a few feet beneath the surface in one of the lakes. The animal did not begin swimming until the boat was quite close. Although the incident occurred during the middle of the day, it is possible that the dolphin was sleeping. Its position before being disturbed was apparently similar to that described for sleeping bottlenose dolphins, *Tursiops truncatus*, which, though principally diurnal in captivity, are also known to sleep during the day (McBride and Hebb, 1948).

SENSES AND TEMPERAMENT

As in other cetaceans, sight and hearing are undoubtedly the senses of greatest importance to the Amazon and river dolphins. While nothing could be learned regarding the extent to which these animals rely upon vision in the course of their underwater activities, it was found that both apparently employed their eyes above the surface on occasion. *Inia* rising to breathe near the boat were sometimes seen to lift their heads higher than usual, thus bringing the eyes out of water, and gave every indication of peering at the boat and its occupants. It was further noted while watching dolphins from the raft at the entrance of the channel

to the Amazon that individuals approaching the channel from either direction would frequently surface once to several times prior to entering, or even mill around at the entrance, rising at short intervals, and then rush through at great speed into the open water of either the first lake or river. Their actions in such instances gave the impression that they were cognizant of their vulnerability in passing through the narrow channel and were looking above water for possible sources of danger before "running the gantlet," so to speak. Many individuals of *Inia* did swim through the channel at normal cruising speeds, not infrequently coming to the surface for air close to the raft despite the presence of an observer. It may be significant, however, that these were mostly small individuals who tended to be less wary than the large adults.

The use of the eyes above the water is also apparently natural behavior among some other cetaceans in the wild, as indicated by the reports of killer whales scanning ice floes for seals (Norman and Fraser, 1949) or bottlenose dolphins herding mullet toward a high bank of an estuary to facilitate their capture (Kritzler, 1952). Experiences with captive bottlenose dolphins (McBride, 1940) and a pilot whale (Kritzler, 1952) have shown that these animals apparently possess relatively keen sight in air.

The murkiness of the waters inhabited by the Amazon dolphin and its diminutive eyes are suggestive of the fact that hearing may be of relatively greater importance to it than vision. Two incidents that occurred while inias were being watched attest to the acuteness of underwater hearing in this species. On one occasion an attempt was made to shoot a specimen with bow and arrow. The arrow landed about 5 feet behind the animal just after it had submerged and was perhaps already 2 or 3 feet below the surface. The instant the arrow struck the water the dolphin lurched suddenly forward and swam off at top speed. Another time a large individual watched from a drifting canoe, surfaced to breathe just as a chain in the bottom of the boat was accidentally brushed and made a very slight rattle. The bouto, although fully 25 yards off, immediately responded to the sound with a convulsive jerk of its body and instantly plunged beneath the surface.

Comparable observations relating to the sense of hearing in *Sotalia* were not made but, in keeping with what is apparently true of cetaceans in general, their auditory sensitivity is undoubtedly of a similarly high order.

McBride (1956), Kellogg *et al.* (1953) and Schevill and Lawrence (1956) have provided evidence bearing on the fact that bottlenose dolphins can and do employ echolocation as a means of orientation. That *Inia* might also rely to some extent on this method of localizing objects in the turbid waters of their habitat arose as a possibility during attempts to net specimens. The net used was about 100 yards long and 10 feet deep and had meshes approximately 2 inches square. It was ordinarily set in the lakes at right angles to the shoreline in areas frequented by the dolphins. Individuals that ventured close to the net invariably seemed to become aware of its presence well before they were in any danger of hitting it and would pass around or below it. On one occasion, when the net was stretched across the channel a short distance above the river, dynamite was exploded underwater in the vicinity of an *Inia* entering the channel in the hope that the dolphin would strike the net in its confusion. Although visibly disturbed by the blast, the animal still avoided the net by swimming over the top at a point between floats where it hung several feet below the surface. The closest an individual came to being ensnared was once when the net was being slowly towed into a new position with an outboard motor boat. An *Inia* surfaced about 25 yards off and swam directly toward the net, submerging shortly still on the same course. A few moments later it burst excitedly to the surface broadside to the net and 4 or 5 feet away, then dove again and swam off without touching the net. It is probable that the porpoise was no closer than 6 feet from the net when it began to turn, and even at this relatively short distance it seems doubtful that the dark-colored meshes would have been visible to it. These observations suggest that the dolphins perceived the presence of the net by some means other than vision, and the possibility that active sonic signals were involved seems worthy of consideration.

No such presumptive evidence for echolocation in *Sotalia* was obtained, but fewer and less critical observations were made in their case.

Larger inias seemed to be rather suspicious of boats and seldom approached or could be approached nearer than about 50 yards. We were told that they were often shot at by local persons, which may have been a factor in explaining their shyness. Despite their reticence to allow too close an approach, the animals seemed to possess an innate sense of curiosity. It often happened that a person just drifting quietly in a canoe on one of the lakes would shortly be surrounded by a group of dolphins, although none might have been evident in the immediate vicinity earlier. This inquisitiveness was clearly evidenced on an occasion when two members of the party, swimming in a cove in one of the lakes, were investigated by a pair of boutos that were seen approaching from some distance away. The animals were unmistakably interested in the swimmers and remained close by for a number of minutes, surfacing several times within 25 or 30 yards of the humans.

Small inias were much tamer than the large adults. It was not uncommon for individuals approximating 4 feet in length to surface time after time within 12 to 20 feet of a boat, and they could be trailed at a fairly short distance, even in a motor boat, without taking alarm.

Less was learned of the temperament of *Sotalia* both because of their smaller numbers and the fact that they were ordinarily more difficult to observe, since they tended to move about more rapidly than did *Inia*. One general impression gained, however, was that they were less inquisitive than the Amazon dolphins.

ACTIVITY AND MOVEMENTS

Amazon and river dolphins were seen at nearly all hours of the day in both the lakes and the Amazon, although they appeared to be more in evidence during the early morning and late afternoon than through the middle of the day. In the lakes, a greater number of dolphins seemed to be present in the middle of the day on overcast or rainy days than on hot, bright ones, suggesting that weather conditions may have some effect on their movements or activity in such quiet waters where surface temperatures may become uncomfortably high.

Nocturnal activity of Amazon dolphins, which could be recognized in the darkness by their blows, was recorded in the lakes and river. Insufficient data were obtained in the latter to provide any indication as to the extent of dolphin activity in that habitat at night as compared to the daylight hours. On the other hand, observations made on several trips in the lakes between sunset and midnight revealed that activity there was apparently considerably less than during the day. Although suggestive, these findings do not conclusively demonstrate that *Inia* is principally diurnal since there is some reason to believe that the diminished activity in the lakes at night might have been the result of a movement of animals back to the Amazon after dark.

No river dolphins were positively identified in the Amazon or lakes at night, but this may have been at least partly due to the difficulty of detecting their presence in the darkness. None was seen or heard in the stream between 7:30 PM and just before dawn. Although river dolphins might easily have been overlooked at night in the Amazon or lakes, it is unlikely that they would have escaped notice had they been active in the stream, for our camp was situated at the edge of the stream about one-half mile above the lake, and much night collecting was done in the vicinity. There was no evident periodicity in the occurrence of *Sotalia* in the stream during the day.

A marked movement of Amazon dolphins into the lakes from the river was evident in the early morning hours from daybreak until about 9 AM and again in the late afternoon from about 4 to 6 PM, although individuals were sighted passing through the channel into the lakes at other times of the day as well. There were no observable peaks of migration in the opposite direction; the dolphins appeared to straggle back to the river from the lakes irregularly throughout the day. The conspicuous ingress of dolphins into the lakes in the morning and afternoon, coupled with the fact that there appeared to be very little activity in the latter

during the night, is suggestive of the fact that there may have been a general exodus back to the main river after dark, although no direct evidence on this point was obtained. *Sotalia* also seemed to show a similar pattern of movements between the lakes and the Amazon, but in their case it was less pronounced because of the smaller number of animals involved.

In both Amazon and river dolphins individuals of the same size and coloration, either singly or in pairs or larger groups, often reappeared in the same locality and at about the same time on different days. Although positive identification was impossible in any instance, the impression was that the same individuals or groups were being observed on these separate occasions. Such circumstantial evidence suggests that individuals of both species may normally range over a fairly definite area and that there may also be some degree of regularity in their movements. In this regard, Williams (1928) reported observing a school of eight *Sotalia guianensis* almost daily at the same locality in the Kartabo District of British Guiana. The activity range of this group included a stretch of several miles in three rivers, the travels of the animals appearing to be restricted in each river by the presence of rapids. Caldwell (1955) has also supplied evidence of home range in the bottlenose dolphin.

INTER- AND INTRASPECIFIC RELATIONSHIPS

While Amazon and river dolphins were often seen in fairly close proximity, individuals of both kinds never closely intermingled, and no interplay of any sort was ever observed between them. There is a widespread belief among the inhabitants of the Amazon valley that *Sotalia* will attack *Inia*, but no one who had ever witnessed such an incident was encountered in the Leticia area.

On nearly all occasions when dolphins were seen, the number and relationship of the individuals to one another were noted. A breakdown of these data for each form provides some idea of the various kinds of association between individuals that were recorded and their relative frequencies. With regard to *Inia*, solitary individuals accounted for 58 per cent of the observations. The animals occurred as pairs about 12 per cent of the time, although Bates (1864) implied that Amazon dolphins typically associate in pairs. A number of pairs that were noted consisted of a large adult and a small individual, and were assumed to be mother and young. Cabrera and Yepes (1940) note that the offspring is believed to accompany the parent for a prolonged period, until almost as large as she. In other pairs, the individuals were of approximately equal size. In some cases both were small, averaging about 4 or 5 feet, but in others the two individuals were 7 or so feet in length. A rather loose relationship appeared to exist between the members of a pair. The animals frequently swam off on separate courses and very rarely surfaced to breathe in unison. This was true even in those pairs considered to be a cow and her calf, for on several occasions very small inias were observed for long periods of time before being joined by an adult. Frequently, too, equally small individuals were encountered that showed no sign of being associated with an adult during the time they were in view.

In approximately 16 per cent of the observations, Amazon dolphins were in groups of three, and about 14 per cent of the time from four to six individuals were present in the same area. Members of such aggregations were usually well dispersed over an area of some 200 or 300 yards or more in diameter, although at times when apparently feeding the individuals might be more closely associated. Usually the dolphins appeared to pay no particular attention to one another, but one instance was recorded in which some interplay between the animals of such a group occurred. About 5 PM one afternoon two members of the party were passing through the lakes en route to camp when they sighted a group of five inias. One of these, possibly an animal that had been stunned with dynamite a few hours before but had escaped, was obviously sick or injured and lay at the surface listing heavily to one side. The other individuals were swimming closely around it, their behavior indicating excitement and interest. They made no actual attempt to assist the injured individual in the interval between the time the group was first noticed and the boat drew

near enough to frighten them away. Ross Allen also reported that captive inias tied by the tail near shore would attract other individuals, who would approach to within 50 feet of the tethered dolphin and remain in the near vicinity for several hours. Instances of apparent solicitude of adult dolphins toward one another have been reported for other species (Hubbs, 1953; Siebenaler and Caldwell, 1955), but it is not certain whether the observations mentioned for *Inia* should be interpreted as behavior of this type or merely attributed to curiosity on the part of the animals. Cabrera and Yepes (1940) noted that females exhibit great concern for their young and should the latter be captured by fishermen, will follow the boat that carries it.

River dolphins seemed to be rather more gregarious than the boutos. Forty-one per cent of the observations on this form were of lone individuals. In approximately 22 per cent of the cases, the dolphins were in pairs, and in 32 per cent, in groups of three. Only in one instance were as many as four or five *Sotalia* seen in the same vicinity, although it was stated by Gervais (*in* Castelnau, 1855) that in the upper Amazon *Sotalia fluviatilis* occurred in herds of 20 or 30 individuals. The aggregations of river dolphins gave the impression of generally being much more closely knit than was the case with *Inia*. The members of a pair or group of three often swam in very tight formation and frequently rolled in nearly perfect synchrony, the animals appearing to be almost touching sides as they came into view above the water. The individuals comprising most pairs or triads showed little size variation. In one instance, however, a group of three was noted that consisted of two large animals and a noticeably smaller one. The latter consistently trailed the others, rolling in their wake.

It seems likely that the groupings observed among the two kinds of dolphins possessed a certain degree of stability in that the same individuals remained together for some periods of time. Evidence favoring this assumption is the fact, previously mentioned, that what were apparently the same pairs or larger groups were seen on different occasions during the period of the study.

FEEDING BEHAVIOR

Little was learned of the respective feeding habits of *Inia* and *Sotalia*, and this was of necessity inferred from the behavior of individuals at or near the surface. Amazon dolphins seen rolling in the characteristic high-arched manner were assumed to be engaged in feeding. At such times the movements of the dolphins were hurried and excited, contrasting to their usual more leisurely and aimless behavior. The animals apparently hunted at some depth, for the surface of the water seldom was roiled between one roll and the next. The manner in which they pursued fish is of course conjectural, but one observation indicated that they may sometimes approach the prey rather slowly. On this particular occasion, an *Inia*, rolling frequently in a circumscribed area along the zone of emergent vegetation bordering the channel, was being watched from the raft less than 15 feet distant. A short time after the animal had disappeared following a roll, a small fish jumped clear of the water near where the dolphin had submerged. A moment later the gaping jaws of the latter slowly rose above the surface at almost the exact point where the fish had leaped. The open jaws wavered erratically for a second or two, then slid quietly back beneath the water. The events suggest that the dolphin had been slowly approaching a fish lying near the surface from below, and at the last moment the intended victim had become alarmed and jumped to escape. If the dolphin had been rapidly pursuing the fish, its momentum would certainly have carried more of its body out of the water.

Feeding individuals tended to remain for more or less extended periods in the same restricted area, frequently near the edge of the flooded jungle, in coves, or opposite points. In a number of instances, members of a pair or larger group were seen rolling within a few yards of one another without showing any signs of animosity when at the surface. The greatest incidence of feeding activity in the lakes was observed during the early morning and late afternoon, which might have been indicative of the occurrence of two major feeding peaks during the day. The coincidence of these periods of supposedly heightened feeding

activity with those of pronounced movements of dolphins into the lakes from the Amazon suggest that the latter were perhaps chiefly alimental in nature.

Several times *Inia* that were apparently in pursuit of fish were seen swimming with great rapidity just beneath the surface. Often small fish were observed leaping out of the water just ahead of the dolphin. Such spectacular, but brief, chases were almost always confined to open waters, although rarely they continued into the flooded jungles for a short distance. The apparent avoidance of the inundated forests by the dolphins may be related to their possible use of echolocation in food-finding, since the effectiveness of localizing fish by reflected sounds would certainly be much less in such situations with numerous underwater obstacles present than in more open water.

Fish were the only kind of food organisms Amazon dolphins were seen to pursue. Although the kinds of fishes eaten could not be determined, it was noted that all those seen to jump in apparent effort to escape pursuing dolphins were under a foot in length, most appearing to be no longer than 6 or 7 inches. These observations may indicate the size range of prey that *Inia* typically prefer.

Although *Sotalia* always rolled to breathe, individuals in some cases were seen to roll faster than was usual. Since there was no evidence that they were disturbed by human presence or other factors, it was supposed that they were engaged in feeding. Though no actual data were obtained as to the nature of their food, they are probably exclusively piscivorous. The stomach of a specimen of *Sotalia guianensis* examined by Williams (1928) contained only fish remains despite the abundance of large shrimps in the waters from which the dolphin was collected.

On one occasion Allen watched a river dolphin come to the surface against the current in the Amazon and remain there with nearly its entire body exposed for perhaps a minute. During this interval its jaws appeared to be moving as if something was being devoured. During his second stay in Leticia, Allen also observed similar behavior in *Inia*, noting that "A number of times we watched them eating fish on the surface of the water." Cabrera and Yepes (1940) also mention this activity in the Amazon dolphin.

Acknowledgments.—I am indebted to Florida's Silver Springs, and especially to William B. Ray and Ricou Browning, for the opportunity of accompanying the expedition and for the numerous facilities put at my disposal. Particular thanks are due E. Ross Allen, who participated in most of the field work during the first expedition and most generously made available certain observations and materials accumulated during his second trip to the region. Acknowledgment is also made to the other members of the first expedition, Charles Hooper, Reed Parham, Bruce Mozert and Sid Latham, for their help in various ways. The photographs of the captive *Inia* and *Sotalia* skull were made by David K. Caldwell, and Esther Coogle assisted in the preparation of the map. W. E. Schevill kindly read an earlier draft of the manuscript and offered a number of valuable suggestions, and Dr. Remington Kellogg provided me with certain information regarding nomenclature. Financial aid was received from the Department of Biology, Florida State Museum, and Graduate School of the University of Florida.

Summary.—The Amazon dolphin, *Inia geoffrensis*, and river dolphin, *Sotalia*, were studied in the vicinity of Leticia, Colombia, from February 19 to March 2, 1956. On the basis of individuals seen, *Inia* outnumbered *Sotalia* in the ratio of about 2:1. Observations suggested some differences in habitat preference between the two forms.

Data on coloration, weight, body and skull measurements, and tooth counts are given. The rather wide range of individual color variation in *Inia* appears to be correlated with age. Present evidence seems insufficient to conclusively settle the taxonomic status of *Sotalia* in the Amazon drainage. It appears that the differences ascribed to the three named species can with equal justification be interpreted as being merely age variations of a single form.

Amazon dolphins surfaced horizontally to breathe when moving at their usual leisurely

pace but rolled to breathe when swimming rapidly or when presumably feeding. *Sotalia* cruised at a greater speed and invariably rolled when breathing.

The dolphins apparently employed vision above water, and evidence for acute underwater hearing and possible use of echolocation was obtained in the case of *Inia*. Young of the latter were less shy than full grown individuals. *Sotalia* seemed to be less inquisitive than *Inia*.

Both dolphins were seen at nearly all times of the day in the various habitats studied, but only *Inia* was actually known to be active at night. Rather regular daily movements of individuals between lakes and the main river and circumstantial evidence for home range were recorded for both.

No social interaction between *Inia* and *Sotalia* was observed, although individuals of both kinds were often seen in close proximity. Pairs and larger groups of *Sotalia* appeared to be more closely knit than similar associations of *Inia*. A possible instance of cooperation at a rather low level was noted in the latter.

Amazon dolphins were seen to pursue fish, observations indicating that they may catch their prey by slow stalking as well as by rapid direct pursuit. Individuals of both dolphins were seen while apparently consuming food at the surface.

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A NEW HARBOR PORPOISE OF THE GENUS *PHOCOENA* FROM THE GULF OF CALIFORNIA

BY KENNETH S. NORRIS AND WILLIAM N. MCFARLAND

On March 18, 1950, a single bleached skull of the porpoise described in this paper, was found by the senior author, on the beach above high tide line, along the north shore of Punta San Felipe, in the northern Gulf of California, Mexico. This skull is designated as the type specimen. Two other skulls of the species were available for study. These were obtained by James Warren and Paul Kellogg during December, 1951, at San Felipe Bay, Baja California Norte, Mexico, and are considered paratypes.

Seth Benson, of the Museum of Vertebrate Zoology at Berkeley, California, first noticed the striking differences that the type series shows, when compared with skull of *Phocoena phocoena* (auct. *P. vomerina*) in the MVZ collection. With this stimulus we have tried to obtain specimens of the entire animal, but have been unsuccessful thus far. We have, however, seen it alive, close at hand. On April 28, 1955, the senior author and James S. Long sighted what must have been *Phocoena sinus*, about 8 miles NE of Punta San Felipe, in the Gulf of California. This locality is a short distance out into the Gulf from the type locality. Three animals were seen. They were slightly less than 5 feet in length. Each animal was a uniform brown color dorsally and had a small triangular dorsal fin. Their blunt snouts were once observed. All were quite wary and were seen only briefly before they submerged. Our attention was first called to the animals by their sharp, loud breathing.

The field journal of the senior author contains the following notation on January 22, 1951: "Topolobampo Bay, Sinaloa, Mexico. The others (Boyd W. Walker and George A. Bartholomew of U.C.L.A.) had done some poisoning in a mangrove lagoon. They caught a few fish, mostly anchovies. When the dead fish drifted down the lagoon with the current they said the water was boiling with snappers taking the anchovies. They saw two bay porpoises (*Phocoena*) with their backs and blowholes out of the water, in one of these

lagoons. The animals inch-wormed themselves rapidly into deep water when the boats approached." Unfortunately, Dr. Bartholomew cannot recall the incident with enough precision to verify the identification, so the record must remain doubtful. He remembers only that the animals in question were small.

The junior author, on February 7, 1953, in company with several students from U.C.L.A., observed two small porpoises in close company in very shallow water in Puerto San Carlos, Sonora, Mexico. The animals were dark in color with a small triangular dorsal fin, but unfortunately it cannot be recalled whether they possessed blunt snouts or not. It is probable that these animals were also *Phocoena*, but the record must remain doubtful.

On May 3, 1956, in Ensenada Bocochibampo, just north of Guaymas, Sonora, Mexico, the senior author and the Chief Collector of Marineland of the Pacific, Frank Brocato, were cruising about ¾ mile offshore when a small porpoise was seen. It was probably of the genus *Phocoena*. Its dorsal surface was very dark and it had a very low triangular dorsal fin. It blew with the characteristic loud puff. Its weight was estimated at 80 pounds. This would tend to support the previous report.

Mickey Vrooman, of the U.S. Fish and Wildlife Service, reported seeing a large group of porpoises in Conception Bay, Baja California, in the month of February, 1956. He was able to verify that the animals were small, possessed no beak, had a small dorsal fin and no white stripes. It would appear that this sight record definitely represents *Phocoena* (personal communication, Raymond Gilmore).

Phocoena has been reported by Scammon (1874) from Banderas Bay, Jalisco, and in the estuary of the Piginto River, Jalisco, Mexico. These were sight records and Scammon considered them identical with the *Phocoena* of the Pacific coasts of California, Oregon and Washington. Nelson (1899) reported *Phocoena* from the nearby Très Marias Islands. He said: "Porpoises supposed to belong to this species were common around the shores of the Très Marias Islands and also in bays and mouths of streams or lagoons along the coast of the mainland. They were seen in the belt of shallow discolored water within a short distance of shore. As soon as blue water, with a depth of over 40 fathoms, was reached the other porpoise (*Prodelphinus longirostris*) was encountered. The common porpoise was seen in schools of 10 to 40 individuals, swimming in loose order. At Maria Madre they came into the shallow bay in front of the settlement in the early morning and followed close along shore."

It is evident that the genus *Phocoena* on the west coast of North America is composed of two distinct species, the northern *P. phocoena* ranging from the coast of southern California northward at least to Pt. Barrow, Alaska, and a southern entity, certainly occurring in the upper Gulf of California, and probably extending far south along the Mexican coast. We describe this southern form as follows:

Phocoena sinus sp. nov.
GULF OF CALIFORNIA HARBOR PORPOISE

Type specimen.—Museum of Vertebrate Zoology (MVZ No. 120933, skull only), from the northeast shore of Punta San Felipe, Baja California Norte, Gulf of California, Mexico; collected March 18, 1950, by Kenneth S. Norris. Paratypes are MVZ No. 120934 (cranium only), and USNM No. 303308 (cranium only); collected in December, 1951, at San Felipe Bay, Baja California Norte, Gulf of California, Mexico, by James Warren and Paul Kellogg.

Comparative material.—Twelve skulls of *Phocoena phocoena* from the Museum of Vertebrate Zoology have been examined. Three skulls of *phocoena*, all representing southward extensions of known range, have been examined from collections at the University of California, Los Angeles. Photographs and literature plates of all known species in the genus have been examined.

Diagnosis.—*Phocoena sinus* is a distinct species, in some respects intermediate in morphology between *phocoena* of the temperate and cold water coasts of North America and Europe, and *spinipinnis* and *dioptrica* of the temperate and cold water coasts of South America and outlying islands. *P. sinus* is the smallest species in the genus, at least with respect to the size of the adult skull. It is distinct from *phocoena* in the following ways: In *sinus*, (1) cranium smaller in adult, with a relatively much broader and shorter rostrum; (2) basi-cranial axis deflected downward at a greater angle, in relation to the horizontal axis of the rostrum; (3) foramen magnum relatively larger; (4) maxillary bone not entering the orbit but excluded from it by the lateral margin of the frontal bone, instead of completely covering lateral margin of frontal and entering the orbit; (5) maxillary leaving a relatively larger exposure of dorsal aspect of frontal bones, where the latter contact the supraoccipital; (6) antero-ventral extension of nasal bones covered by mesethmoid; (7) posterior edge of the palate with medial U-shaped indentation, formed of the medial edges of the rounded, roughly triangular pterygoid bones and the ventral extension of the vomer, which enters the palate just posterior to the palatine bones. In *phocoena* the posterior edge of the palate has a W-shaped indention, formed by the pointed, usually acutely triangular pterygoid bones and a central, pointed extension of the palatines, which sometimes cover the ventral extension of the vomer completely, but more often leave it as a small point of bone at their apex; (8) lower maxillary and mandibular tooth count. *P. sinus* differs from *phocoena* in other minor ways that will be discussed in the section of description.

Phocoena sinus appears different from *spinipinnis* in the following respects: In *sinus*, (1) cranium smaller in adult, with relatively shorter rostrum; (2) higher total tooth count, with teeth distributed along nearly the entire margin of mandible and maxillary, instead of with a distinct posterior diastema; (3) dorsal aspect of supraoccipital bones (in lateral view) tilted at an angle of slightly over 20°, instead of in the same plane as the rostrum; (4) maxillary bones exposing smaller relative portions of the frontals on the dorsolateral

surface of the brain case; (5) a more flattened, more asymmetrical and less prominent vertex; (6) posterior margin of palate with U-shaped indentation, instead of W-shaped.

Phocoena sinus appears different from *dioptrica* in the following respects: In *sinus*, (1) cranium smaller in adult; (2) dorsal aspect of supraoccipital bones (in lateral view) tilted at an angle of slightly over 20°, instead of the same plane as the rostrum; (3) posterior margin of palate with U-shaped indentation instead of broadly W-shaped; (4) maxillary portion of palate flat or slightly concave instead of definitely convex; (5) maxillary bones exposing relatively larger portions of the frontals on the dorsolateral surface of the brain case; (6) vertex relatively much smaller; (7) intermaxillaries standing above the maxillaries throughout the length of the rostrum, instead of level with the maxillaries; (8) no evidence of the striking white ventral and lateral coloration of *dioptrica*, though the entire animal has not been examined closely. The data on *dioptrica* listed here are from Hamilton (1941) and from plates kindly supplied to us by F. C. Fraser of the British Museum. Comparative measurements of the four species are given in Table 2.

Description of type specimen.—A fully adult specimen, judging from the complete fusion of the postorbital processes of the frontals and the zygomatic processes of the squamosals, forming complete arches. Also, the intermaxillary bosses are large and overhanging, seemingly indicative of adult condition. Ankylosis is complete between many cranial bones to the point where the sutures are no longer evident. For example, the basisphenoid is completely continuous with the surrounding basioccipitals. The cranium is 211 mm. total length, from the tip of the rostrum to the dorsal point of the foramen magnum. Ratio of width across zygoma of squamosals to total length: 0.637 (see Table 1 for comparisons). Rostrum relatively short and broad. Intermaxillaries stand up above adjacent maxillaries throughout their length, imparting an arched cross section to the rostrum. Vomer entering palate at two points, anteriorly appearing in the mid-palate as a small elongate diamond and posteriorly on the posterior margin of the palate as an oval process. The ventral wings of the pterygoids are missing in the type, but present in the paratype (USNM 303308) in which they are roughly triangular, rounded bones forming a U-shaped margin of the palate in conjunction with the vomer.

In the type the palatine portion of each maxillary is creased by a fissure extending posteriorly from about the mid-point of the anterior insertion of the vomer, down the mid-line of the maxillary, one-third its length.

The mesethmoid defines the nares dorsally and covers the anteroventral extension of the nasal bones along the mid-line. The nasals are crossed horizontally by a well-defined ridge which invades the medial edges of the maxillary bones. The maxillaries are arched upward at the anterior edge of the temporal fossae, exposing the posterior extensions of the frontal bones for a maximum of 12.1 mm. The vertex is markedly asymmetrical, being undercut nearly to the mid-line on the right side, while the left side is solid and only slightly undercut.

The dorsal edge of the orbit is defined by a lateral edge of the frontal bone, the maxillaries failing to enter the orbit by a minimum of 4 mm.

The supraoccipitals slope down sharply from the vertex to the condyles, meeting along the mid-line in a broadly U-shaped furrow. The foramen magnum is large (34.0 mm. along dorsal axis) and egg-shaped, with the apex pointing dorsad. The condyles are large and ventrolaterally placed. The basicranial axis is formed of broad basioccipitals which are joined completely to the basisphenoid and suturally joined to the rather thin exoccipital. The jugular protuberances of the exoccipital are composed of thin ridges of bone, compared to the heavy bosses found in *phocoena*. The indentation of the glenoid fossa is much weaker and smaller than in *phocoena*. The condylar foramen is a deep, open, U-shaped furrow.

Internally a low ridge runs transversely across the base of the cranium at the junction of the basioccipital and basisphenoid. This ridge is much more pronounced than in *phocoena*.

The mandibles are short and stout. The coronoid border is straight and does not bend laterally to form a small flange, as in *phocoena*. The teeth are spade-shaped, with some tendency to exhibit extra cusps on the posterior teeth in upper jaws. Tooth counts and measurements are given in Table 1. See Plates I–III.

TABLE 1.—*A comparison of the type and paratypes of P. sinus*

CHARACTER	TYPE (MVZ NO. 120933)	USNM NO. 303308	MVZ NO. 120934
Skull length	211.0 mm.	226.0 mm.	218.0 mm.
Zygomatic width, across squamosal processes	135.8 mm.		
Greatest breadth at maxillary notches	73.8 mm.	75.5 mm.	77.0 mm.
Length of rostrum, from tip of rostrum to anterior edge of left naris	117.0 mm.	120.0 mm.	117.2 mm.
Ratio: Width/length of rostrum	0.630	0.629	0.657
Height of foramen magnum	34.0 mm.	38.0 mm.	37.8 mm.
Deflection of rostrum*	14.5°	13.5°	13.5°
Depth of skull†	115.0 mm.	122.5 mm.	116.0 mm.
Greatest breadth of brain case across temporal fossae	113.5 mm.	114.5 mm.	113.0 mm.
Shape of pterygoid-palatine-vomer complex‡	——	Broad U	
Exposure of frontals§	11.8 mm.	14.0 mm.	10.0 mm.
Condylar foramen shape	U	U	U

* Deflection of rostrum expressed by angle between horizontal axis of rostrum and a line from midpoint of occipital condyles to tip of rostrum.

† Depth obtained by placing skull on a table and measuring from point of contact of basioccipital to dorsal extremity of vertex.

‡ This refers to the shape described by the bones listed at the posterior edge of the palate.

§ The frontal bones are covered by the maxillary bones except for a margin at their posterior edges. Measurement is widest exposure on right side.

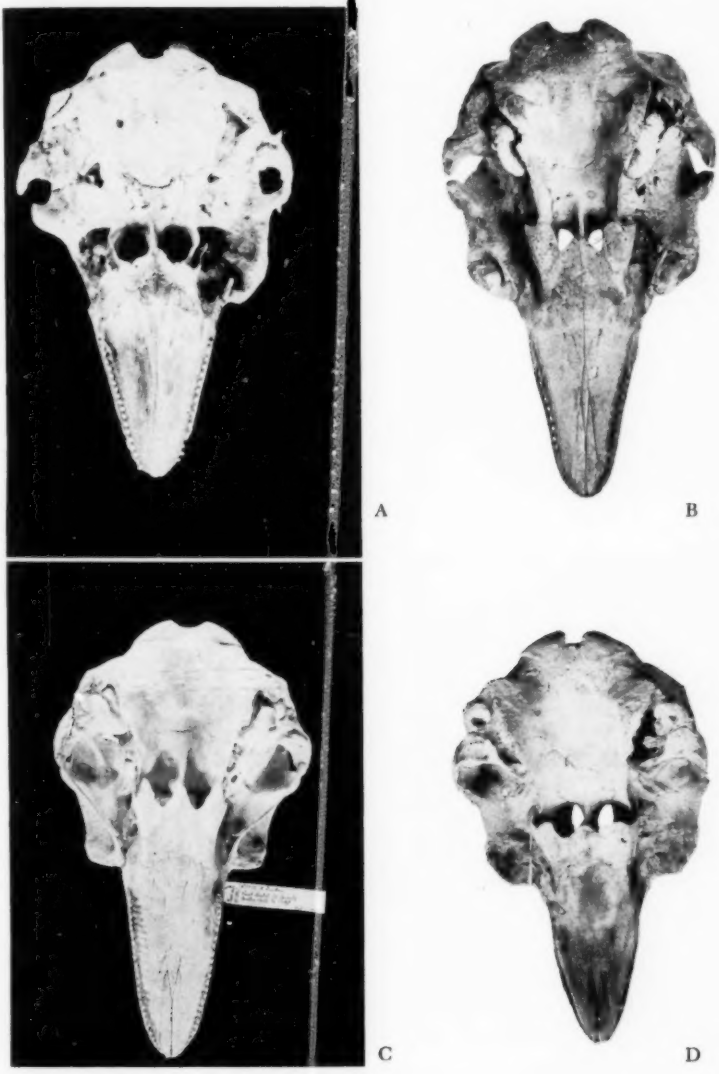

PLATE I

Ventral view of crania: A, *Phocoena sinus* (type); B, *P. spinipinnis* (MCZ specimen described by Allen, 1925); C, *P. phocoena* (MVZ 90341); D, *P. dioptrica* (British Museum specimen described by Hamilton, 1941).

A

B

C

D

PLATE II

Dorsal view of crania: A. *Phocoena sinus* (type); B, *P. spinipinnis* (MCZ specimen described by Allen, 1925); C, *P. phocoena* (MVZ 90341); D, *P. dioptrica* (British Museum specimen described by Hamilton, 1941).

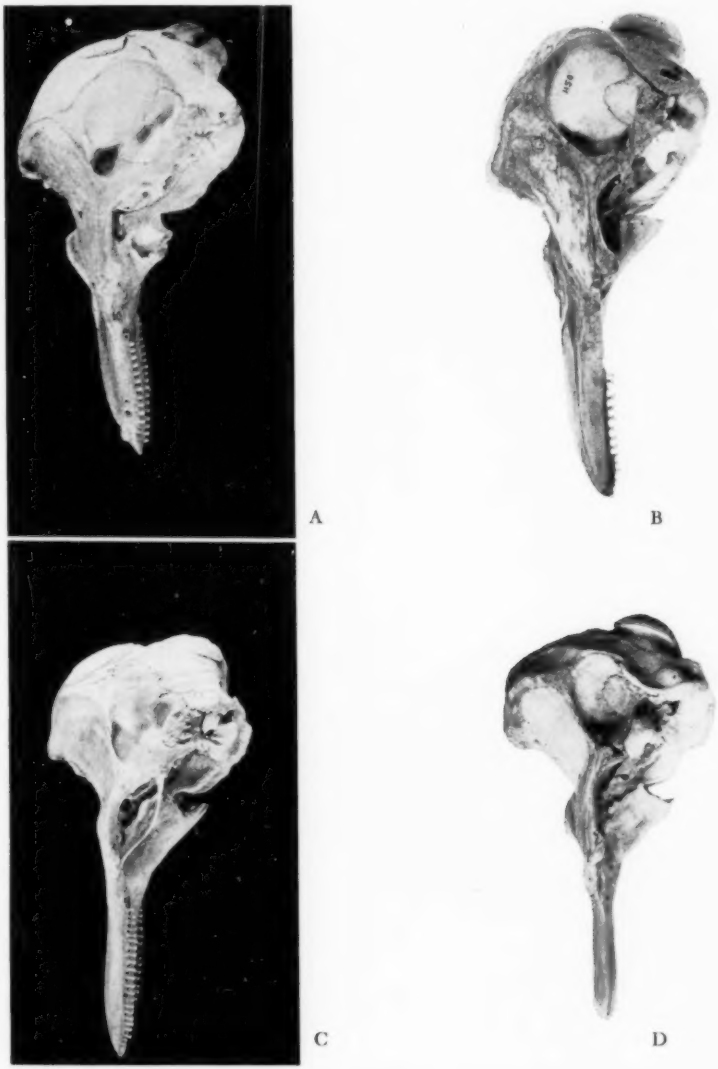

PLATE III

Lateral view of crania: A, *Phocoena sinus* (type); B, *P. spinipinnis* (MCZ specimen described by Allen, 1925); C, *P. phocoena* (MVZ 90341); D, *P. dioptrica* (British Museum specimen described by Hamilton, 1941).

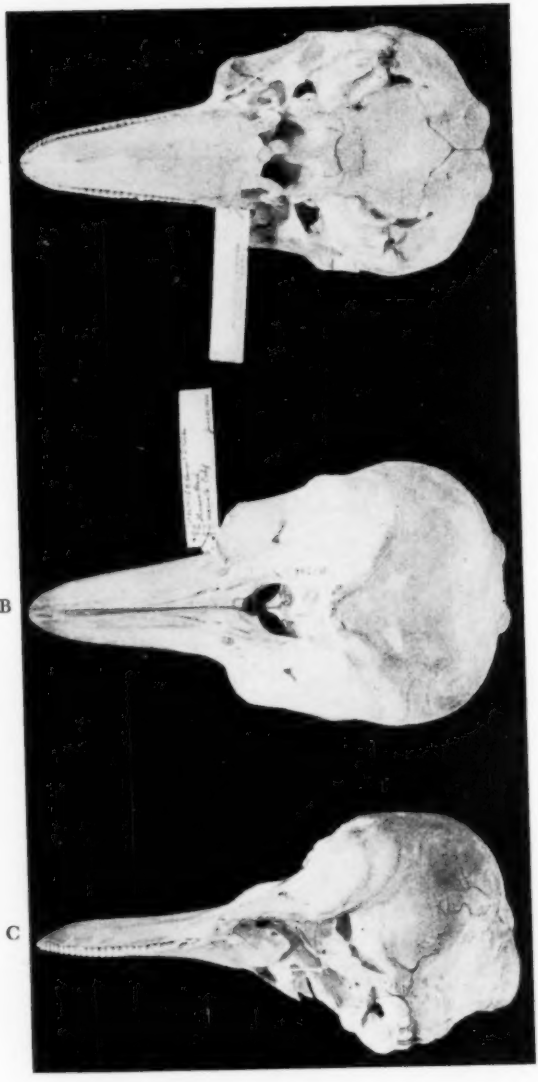

PLATE IV

Juvenile specimen of *Phocoena phocoena* (MVZ 112246). A, ventral view; B, dorsal view; C, lateral view. Note incomplete ossification of bones.

Paratypes.—The two paratypes (MVZ 120934, USNM 303308) are both bleached and cracked skulls which had obviously spent much time on the beach before being picked up. As a consequence some comparisons are impossible. However, where comparison is possible they are remarkedly similar to the type and indicate that the type is not just an aberrant specimen but a representative of a distinct species. The three skulls are compared in Table 1.

Comparisons.—A number of genera have at one time or another been lumped with *Phocoena* as it is presently recognized. For example, Owen (1866) described *Orcella brevirostris* in *Phocoena. Phocoena pectoralis* Peale (1848) of the Hawaiian Islands, appears close to or identical with *Cephalorhynchus heavisidei* Gray. There are many other examples of this sort.

Several small, blunt-snouted delphinids, possessing a dorsal fin and spade-shaped teeth, have been described in the genus *Phocoena.* Of these only three

TABLE 2.—*A comparison of Phocoena sinus, P. phocoena, P. spinipinnis and P. dioptrica*

CHARACTER	*P. sinus* (type)	*P. phocoena**	*P. spinipinnis*†	*P. dioptrica*‡
Skull length, from tip of rostrum to condyles	211.0 mm.	278.0 mm.	273.0 mm.	288.0 mm.
Length of rostrum, from tip to edge of left naris	117.0 mm.	156.8 mm.	141.0 mm.	152.0 mm.
Palate length, from tip of rostrum to median spine of palate	111.6 mm.	169.6 mm.	152.0 mm.	164.5 mm.
Length of tooth row, including alveoli	73.2 mm.	117.1 mm.	79.0 mm.	
Zygomatic width, across squamosal processes	134.5 mm.	149.5 mm.	153.0 mm.	168.0 mm.
Greatest breadth of rostrum at maxillary notches	73.8 mm.	73.7 mm.	83.0 mm.	88.0 mm.
Greatest breadth across brain case at temporal fossae	113.5 mm.	128.0 mm.	127.0 mm.	
Ratio: Width/length of rostrum	0.630	0.470	0.517	0.727
Ratio: Skull width/skull length	0.637	0.537	0.560	
Shape of pterygoid-palatine-vomer complex	U	W	W	Broad W
Widest dorso-posterior exposure of frontals	11.8 mm.	9.0 mm.	25.0 mm.	Slight exposure
Tilting of dorsal aspect of supraoccipital bones with relation to axis of rostrum (in lateral view)	22°	23°	0°	0°
Teeth	20–21 / 18–18	27–28§ / 26–26	16–16 / 17–18	21–21 / 17–17

* MVZ 96089.
† Measurements and counts taken from Allen (1925).
‡ Measurements and counts taken from Hamilton (1941).
§ Alveoli counted in lower jaw.

seem to be valid species. *Phocoena dioptrica* Lahille 1912 and *Phocoena spinipinnis* Burmeister 1865, of the coasts of Argentina, Chile, Peru and certain outlying islands, are now well enough known to be generally accepted. *Phocoena phocoena* (Linnaeus) of the coasts of Europe and the Atlantic and Pacific coasts of North America is the remaining form.

Philippi (1893) described seven forms in the genus *Phocoena* from South America, and none of them seem valid; *philippii* is almost certainly synonymous with *spinipinnis*. True (1903) allocated *posidonia* to the genus *Lagenorhynchus*, and suggested that *P. obtusata* appeared to belong to *Cephalorhynchus*. *P. d'orbignyi* is synonymous with *Lagenorhynchus cruciger* (d'Orbigny and Gervais); *lunata* and *cruciger* were species described by Philippi based solely on sight records and have no validity. True (1903) considered Philippi's *P. albiventris* to be probably synonymous with *Cephalorhynchus eutropia*.

Phocoena storni described by Marelli (1922) from Tierra del Fuego, was described from a single cranium. The animal was differentiated from *dioptrica* as a new species on the basis of a number of proportions and tooth counts. All the proportional differences which separate it from *dioptrica* appear to be related to individual variation, which is great within the genus, or to the apparent old age of the specimen. Tooth counts were taken on one side of the upper jaw only because of missing teeth on the other side. The photograph given shows the alveolar border running a short distance posterior to the last tooth on the counted row. It is probable that the 18 teeth counted do not represent the true total in the intact animal, and the count is of dubious diagnostic value at any rate, from the count of 21 given by Hamilton (1941) for *dioptrica*. We conclude from these facts and examination of a photograph of the type that *storni* represents a synonym of *dioptrica*.

Phocoena vomerina Gill 1865, of the Pacific coast of North America is indistinguishable from *phocoena* of the Atlantic, on the basis of the original description. Adequate samples are now available from both populations for a final solution of the validity of *vomerina*.

Phocoena tuberculifera Gray 1865, from the mouth of the River Thames, is based on a specimen of *phocoena* having a tuberculate dorsal fin. This anomaly seems to occur with fair regularity in the species. A tuberculate dorsal fin is apparently always present in *spinipinnis*.

Phocoena brachycium Cope 1865 and *Phocoena lineata* Cope 1876, appear to be synonymous with *P. phocoena*, Cope's diagnosis being based mainly upon the development of the vomer, a character which we have found to be highly variable in Pacific members of this species. Flower (1883, p. 471) showed this variability to be present in Atlantic populations of *phocoena*.

There has long been a controversy concerning the generic status of the small finless porpoise, *Neomeris phocaenoides* Gray (1846), of the Indian and Pacific oceans. This small animal ranges from the Cape of Good Hope to Japanese waters and appears to be the ecological counterpart of the genus *Phocoena* in the Far East. It is certainly very closely allied to *Phocoena*, having a blunt snout and

spade-shaped teeth. The major separating characters are its finlessness and the relation of the plane of the rostrum to the basicranial axis. The rostrum is bent downward with relation to the basicranial axis at about 45°, while in *Phocoena* this angle is about 30°. Blanford (1891) placed the form in *Phocoena*, while Flower (1883) and True (1889) called attention to the fact that the generic name *Neomeris* was preoccupied by a genus of polyps. However, both workers continued to use this name. Palmer (1899) again called attention to this preoccupation and proposed a new name, *Neophocoena*. However, in 1925, Thomas showed that *Meomeris* had priority, an apparent misprint in Gray's List (1847). Allen (1925), in a discussion of the affinities of this propoise with *Phocoena*, considered it as closely related to *Phocoena*, but more primitive. He retained the genus name of *Meomeris*. Thomas (1925) suggested that since the polyps, originally considered as preoccupying the name *Neomeris*, have been subsequently identified as a species of alga, the name was still available for the porpoise. We accept this nomenclatorial decision, which is very fortunate due to the common usage of the name *Neomeris*. Its relationships are clear and its taxonomic allocation is therefore a matter of particular emphasis of generic or specific categories.

Having thus limited the previously known living representatives of the genus *Phocoena* to three species, we can restrict our comparisons to these species. The general comparisons are listed in Table 2. See also Plates I–III

Miller (1923) discussed the evolution of the cetacean skull, showing how it has become telescoped, particularly by the process of movement of the nares to the top of the head, from the terminal position on the snout. In the Cetacea, he considered complete coverage of the posterior extension of the frontal bones by the overlapping maxillaries to be an advanced state. It is interesting that in *Phocoena* various degrees of coverage of the frontals are found. While there is is a wide individual variation, *P. phocoena* and *dioptrica* have by far the greatest relative coverage of the frontals, of the four species. *P. sinus* and *spinipinnis* are linked by having a rather wide exposure. In this regard, Allen (1925) considered *P. spinipinnis* as a much more generalized form than *phocoena* on the basis of several criteria other than frontal exposure.

The skull of a very young female *phocoena* (MVZ 112246) shows affinities with the southern species that are not shown in any of the adults examined. See Plate IV. Since the animal was picked up on Stinson Beach, (June 25, 1944, by D. Politeo) and was small (length 465 mm. nose to fluke notch; weight 19¼ lbs.) it most likely represents a newborn calf. Evidence of its youth other than its size comes from the incomplete ossification of many bones, such as the pterygoids, and the open sutures connecting others which are normally fused in adults. Even though the skull of this animal is about one-third smaller than any other examined, the posterior exposure of its frontals by the maxillaries is nearly the greatest measured (16 mm.). Proportionately, it is allied to *sinus* and *spinnipinnis* in this respect; Unlike adults of its species the dorsal aspect of the supraoccipitals is nearly flat, like the condition of *spinipinnis* and *dioptrica*.

The ventroposterior extension of the vomer enters the palate in variable amounts in Pacific specimens of *phocoena*, as mentioned. Sometimes it is completely absent from the palate, covered by the palatines. The extension of the vomer into the posterior margin of the palate is relatively greater in the juvenile specimen than in any of the adults. In this respect, the young animal is linked more closely to *sinus* and apparently *dioptrica* than to *spinipinnis*.

These ontogenetic changes in *phocoena* are of interest as they tend to confirm the idea of Allen (1925) that *spinipinnis* is a more generalized form than *phocoena*. We extend this idea to both *sinus* and *dioptrica*, considering both of them and *spinipinnis* closer to the stem stock than is *phocoena*, which is considered consequently as the most highly evolved member of the genus.

Phocoena sinus is allied to the South American members in a number of ways, in particular to *spinipinnis*. Tooth counts for all three forms are low compared to *phocoena*. The wide extent of dorsoposterior exposure of the frontals links *sinus* and *spinipinnis*. Cross sections of the rostra of *spinipinnis* and *sinus* are arched throughout their lengths, whereas *phocoena* has the base of the rostrum flattened due to a depression of the intermaxillaries at that point. Toward the tip of the rostrum the intermaxillaries arch upward forming a rounded cross section. The rostrum of *dioptrica* is seemingly flat throughout its length. *P. phocoena* has the slimmest skull of the four forms, considering the breadth of the brain case at the squamosal processes of the zygomatic arch (zygomatic width) in relation to total skull length. The temporal fossae of *phocoena* are generally smaller than in the three southern species. Although the characters are intermingled in various proportions amongst the four species, we feel that *spinipinnis*, *sinus* and *dioptrica* form a natural group, more primitive than *phocoena*.

The species *phocoena*, *spinipinnis* and *dioptrica* are approximately of equal size when adult; *sinus*, judging from the skull length of the adults and the small size noted in the sight records, is probably a considerably smaller animal.

Zoogeography.—Allen (1925) described the known range of *spinipinnis* as follows: "in the cooler waters off the South American coast from the La Plata region, around Cape Horn, and northward in the Humboldt Current to northern Peru, a range closely similar to that of several other marine vertebrates as shown by Dr. R. C. Murphy (1923)." The northernmost record on the Pacific coast is Payta (or Paita), Peru, near the Ecuadorian border. This locality is approximately 2,450 airline miles south of the southernmost sight record for *Phocoena* (probably *P. sinus*) and 3,300 miles south of the type locality of *sinus*.

P. dioptrica is known only from the South Atlantic coast of South America (Rio La Plata, Rio Santiago, Falkland Islands, South Georgia; see Hamilton, 1941). The species is little known and its range probably far exceeds that reported.

P. phocoena ranges throughout the littoral waters of Europe to the North Sea and into the Arctic Ocean. It is quite common around the British Isles. To the South it extends into tropical waters, having been taken at Dakar, West Africa,

by Cadenat (1949). A probable subspecific differentiate, *P. p. relicta,* occurs in the Black Sea (Zalkin, 1938). A recent Russian paper (Kirpichnikov, 1952) was unfortunately not available to the authors. In the Western Atlantic it occurs along the coast of North America from Davis Strait southward to at least the Delaware River. In the Pacific it ranges from the northern tip of Alaska at Point Barrow (see Miller and Kellogg, 1955) to the San Pedro Channel in southern California. Previous to this report the southern record has been considered Rockaway Beach, San Mateo County, California (Orr, 1937). Through the courtesy of G. A. Bartholomew of the Department of Zoology at the University of California, Los Angeles, we obtained three specimens of *phocoena* from the osteological collection, all of which represent considerable southward extensions of known range. UCLA cranium No. 1184 was found on the beach at Point Mugu, Ventrua County, California, by Loye Miller in March, 1931. UCLA cranium 1440, was picked up at Hyperion Beach, Los Angeles County, California, also by Dr. Miller in 1934. The third and southernmost record (UCLA 1439) is a female captured by fishermen in the San Pedro Channel off San Pedro, California. The animal was exhibited in the window of Bernstein's Fish Grotto in Los Angeles for a few days before being given to Miller by J. R. Pemberton. These records seem to represent an extension of range due to unusual conditions, as the species is not a common resident until one goes northward to the vicinity of San Francisco Bay. All three specimens are large adults. UCLA 1440 is as large as the largest animal measured in the MVZ collection (MVZ 21509, 289 mm. condylobasal length). The heavy ossification of the vertex in this UCLA specimen and the great width of the rostral base (94.5 mm.) suggest old age. It is our feeling that these range extensions represent old animals that have wandered far beyond their normal range. Fraser (personal communication) states that Cadenat's specimens from Dakar are all larger than any of 33 skulls from British waters. The largest Dakar skull is 300 mm. total length.

With the possible exception of *phocoena* in subtropical waters at Dakar, West Africa, the ranges of *dioptrica, spinipinnis* and *phocoena* are strongly antitropical in character. Thus, the discovery of a species of *Phocoena* in the subtropical waters of the upper Gulf of California and probably extending into truly tropical seas around the Très Marias Islands and Banderas Bay, Jalisco, Mexico, is unexpected and unusual. This form shows its closest affinities with the distant South American species and not with the geographically nearest form (*phocoena*) which occurs 325 airline miles north of the type locality and about 1,500 miles along the coastline.

With the passage of geologic time two factors have been at work that could have given rise to *P. sinus*. First, during a time when seas were cooler, many temperate species of marine animals have crossed the equatorial barrier, resulting in bitemperate distributions. After discussing a number of fish species that seem to have crossed the equator, perhaps by descending to deep cool waters, Hubbs (1952) discusses the passage of surface-bound forms. He says:

Many other antitropical fishes of the temperate zones, including most of the pantemperate types, have attributes that lead us to believe that they crossed the tropics when surface waters were considerably cooled, presumably during late Pleistocene time. Ecologically they are surface-bound; therefore incapable of transgressing equatorial water by the cool deep-water routes. That they crossed the tropics during the last cold period of the Pleistocene is suggested by their incipient speciation.

In this category of surface-bound recent transgressors of the tropics we must include such shore-pelagic fishes as the sardine or pilchard genus *Sardinops* (of California, Japan, and Chile, and Australia and New Zealand, and South Africa); the round herrings of the genus *Etrumeus* (of the western North Atlantic, California, Hawaii, Japan, Australia, and South Africa); the anchovy genus *Engraulis* (of Europe, Japan, South Africa, and Australia and New Zealand); the similar anchovies of California, Peru and Chile, and Argentina, which, as I shall presently show, constitute a distinct genus; the even more strikingly pantemperate jackmackerel (*Trachurus*) and chub mackerel (*Pneumatophorus*) groups; the saury genus *Scomberesox* (of North Atlantic and South Temperate waters); the species of *Seriola* related to S. *dorsalis*; *Centrolophus*; several tunas (Thunnidae) and tuna-like fishes; also *Alepisaurus* and various other rather pelagic types.

As emphasized by Berg (1933) not only these fishes, but also various other organisms almost certainly had a surface-water connection between the northern and southern hemispheres at a geologically very recent time, very probably, in large part, during the last period of continental glaciation. Notable examples are sea lions (Otaridae), right whales (*Eubalaena*), and the giant kelp *Macrocystis*, which is said to be represented in both hemispheres by the same two ecotypic varieties of a single species.

To this list mentioned by Hubbs, Ekman (1953) adds several other fishes as well as citing data on the distribution of invertebrates. In addition he mentions the "Bipolar" (= Antitropical) distribution of the genus *Macrorhinus* (sea elephants) and the genus *Arctocephalus* (fur seals) all of which have specific differentiates in the North and South Temperate Hemispheres. Ekman further stresses the importance of the Eastern Pacific as a route of migration during the Pleistocene Epoch to explain these distributions (see Ekman, 1953, p. 248).

Very probably, a form ancestral to *P. spinipinnis* crossed the tropical latitudes at such a time, when the South American Humboldt current (in which *spinipinnis* now occurs) converged with an extension of a northern counterpart (*see* Hubbs, *op. cit.*). It should be stressed that this possibility is even more probable in light of the presence of *sinus* and *phocoena* in tropical or at least subtropical waters. The presence of *phocoena* at Dakar is best considered as a penetration of a temperate form into a subtropical region. Ekman (1953, p. 55) considers the Dakar area as a transitional faunal area between the tropical and temperate regions. In addition, it is interesting that *Neomeris phocoenoides*, the Western Pacific and Indian Ocean generic counterpart of *Phocoena*, is strongly tropical in its distribution. Such evidence suggests the possibility that the ancestral forms of the genus *Phocoena*, or even its earliest members, could withstand higher temperatures. If this was the case, *P. sinus*, or more probably its ancestors, might readily have penetrated the equatorial regions during the Pleistocene, only retreating at the close of this epoch or during one of the interglacial periods. The affinities of *sinus* to the South American members of the genus, rather than

to *phocoena*, are thus readily explained by the action of continental glaciation and its effect upon the surface water temperatures. Lowering of a few degrees would be sufficient to explain the present distributions.

The second factor which may have acted in the evolution of *P. sinus* is the configuration of sea and land forming the Gulf of California. This Gulf has acted as a *cul-de-sac* in trapping and isolating a considerable number of temperate species in its upper reaches, as faunas became displaced during the Pleistocene (see Hubbs, *op. cit.*). Many of these forms have been recorded in the region of upwelling adjacent to Angel de la Guarda Island. *Sebastodes sinensis*, the only member of this bitemperate genus in the Gulf, occurs only at this location. The fish collections at the University of California, Los Angeles, collected by Boyd W. Walker and students, contain such temperate fishes from this region as *Triakis semifasciata*, the leopard shark, and a skate which is identical, or nearly so, with the California species, *Raja inornata*. The sargo, *Anisotremus davidsoni*, and the black croaker, *Sciaena saturna*, also have restricted populations in the upper Gulf of California. The northern spiny lobster, *Panulirus interruptus*, is also isolated in the vicinity of Angel de la Guarda Island. This list of isolated forms could be extended and would include several phyla.

The sight records of Scammon and Nelson, cited earlier, would extend *P. sinus* beyond the confines of the Gulf of California. However, in the absence of specimens from these regions, the comments about *sinus* by Mexican fishermen at San Felipe, near the type locality, are most interesting. These men know the little porpoise well and speak of it leaving the upper Gulf in the summertime. They say it is found in the vicinity of Los Angeles Bay and Angel de la Guarda Island at this time. During the summer months the upper Gulf becomes very warm (surface temperatures as high as 88°F.) while the upwelling area near Angel de la Guarda Island remains cool. However, if *sinus* occurs as far south as Jalisco, Mexico, a summer migration from this region to the cool water area at Angel de la Guarda, as might be the case with the northern Gulf population, would be a spectacular phenomenon and would probably have been noticed before this time.

It would appear possible that after the ancestor of *P. sinus* had reached the Gulf of California from South America and waters began to warm with the retreat of the continental ice sheets, the porpoise retreated northward with the cooler waters and was isolated in the upper Gulf.

The possibility exists that *sinus* was derived from ancestral *phocoena*, as the latter species moved southward with cold water, and became trapped in the Gulf as the parent stock moved northward when waters warmed again. In this case *sinus* would be considered as a slightly paedogenic or "larvalized" form because it resembles the postembryonic *phocoena* considerably more than it does the adult. However, we tend to favor the idea that *sinus* was derived directly from a South American form, because it resembles *dioptrica* and particularly *spinipinnis* more than it does even the young of *phocoena*. Perhaps

proof or disproof of this theory will come when a whole specimen of *sinus* is obtained. If *sinus* possesses a peculiarly shaped tuberculate dorsal fin similar to that of *spinipinnis* and similarities of the axial skeleton, the historical continuity of the two forms must then be considered highly probable.

We wish to thank Dr. Seth Benson for loaning us specimens in his care and for his generous assistance with other phases of this study. Dr. Carl L. Hubbs has helped in many ways, particularly in suggesting the specific name which we have given the species. Dr. F. C. Fraser has assisted by obtaining the plates of *P. dioptrica* and reviewing the manuscript. Drs. G. A. Bartholomew and Boyd W. Walker have loaned specimens and records in their care. We thank James Warren for providing us with two paratypes of *P. sinus* and for access to his field records. Dr. Barbara Lawrence of MVZ kindly had photographs prepared for us of the skull of *P. spinipinnis*.

Contribution No. 2, Marineland of the Pacific Biology Laboratory.

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THE PREHISTORIC DISTRIBUTION OF THE OPOSSUM

BY JOHN E. GUILDAY

The opossum, *Didelphis marsupialis virginiana* Kerr, is widely distributed throughout the eastern United States. It occurs as far north as southern Ontario (Peterson and Downing, 1956). Hamilton (1943) gives its range as including Connecticut, Rhode Island, Massachusetts, southern Vermont and southern New Hampshire. It does not occur in the Adirondack Mountains nor in the uplands of New England.

The opossum has migrated northward within historic times. Along the Atlantic coast the animal was formerly found no further north than the Hudson

River Valley. Goodwin (1935) stated that the spread of the opossum into Connecticut took place "within the last twenty years." Brayton (1882) wrote that the animal "is not uncommon in central and southern Ohio, Indiana, and Illinois . . . the northern portions of these states are not so congenial to it." Rhodes (1903), in discussing the distribution of the opossum in Pennsylvania, said: "Variably abundant in middle and southern counties in all situations except in the mountain summits; extending northwards in lessening numbers along the river valleys to and into New York State from Lake Erie to the Hudson River. . . . with the deforesting of the mountains invading large areas of the Alleghanian (*sic*) regions previously unknown to them."

A general picture of the prehistoric distribution of the opossum in the northeastern United States may be had by plotting the geographical distribution of records of opossum bones associated with the Indian occupation of the area (Fig. 1).

The record of a prehistoric occurrence of an animal from an archeological site may, on occasion, be based upon a chance association of modern bones (especially those of burrow-frequenting species) in an aboriginal context. This is usually a readily recognizable situation, however, and, with the possible exception of records from rock shelters, is not common. The *absence* of an animal's remains from any given site may also be fortuitous. As an isolated record such negative information is valueless. However, when archeological faunas from many sites in the same general area are compared, and remains

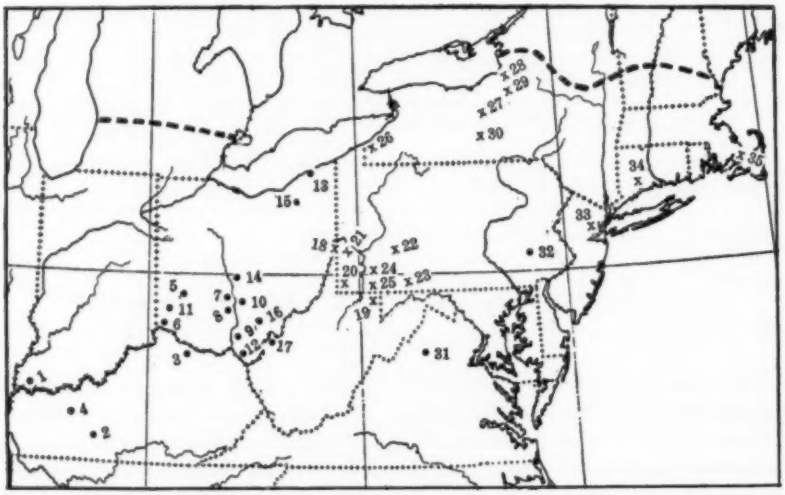

FIG. 1.—Distribution of archeological sites showing presence or absence of associated opossum remains in eastern United States. Numerals refer to sites listed in the tables; •, reported opossum remains; x, no opossum remains reported; ----, approximate present northern limit of distribution.

of a particular animal are consistently absent, this type of information becomes highly suggestive.

TABLE 1.—*Archeological sites from which opossum remains have been reported*

MAP NO.	STATE	SITE	REFERENCE
1	Ind.	Angel Mounds	Adams, M.A. diss., Dept. Anthrop., Ind. Univ., 1949
2	Ky.	Mammoth Cave	Nelson, Anthrop. Pap., Amer. Mus. Nat. Hist., 22: 1–73, 1947
3	Ky.	Fox Farm	Smith, Anthrop. Pap., Amer. Mus. Nat. Hist., 6: 173–241, 1910
4	Ky.	Indian Knoll	Webb, Univ. Ky. Rept. Anthrop. Ethnol., 4(3), 1946
5	Ohio	Anderson	Brainerd, Abst. diss. No. 24, Ohio State Univ., 1937
6	Ohio	Madisonville	Hooton, Papers Peabody Mus. Arch. Ethnol., 8: 1–137, 1920
7	Ohio	Baum	Mills, Ohio Arch. Hist. Quar., 15: 45–136, 1906
8	Ohio	Cramer	Goslin, Ohio Arch., n.s. 4, 1954
9	Ohio	Feurt	Goslin, Ohio Indian Relic Coll. Bull. 25: 16–22, 1950
10	Ohio	Gartner	Griffin, THE FORT ANCIENT ASPECT, Univ. Mich. Press, 1943
11	Ohio	Campbell Id.	*Ibid.*
12	Ohio	Proctorville	*Ibid.*
13	Ohio	Fairport Harbor	Morgan and Ellis, Ohio Arch. Hist. Quar., 52(1), 1943
14	Ohio	Kettle Hill	Goslin, Ohio Jour. Sci., 55 (6), 1955
15	Ohio	Twinsburg	*Ibid.*
16	Ohio	Cantor Cave	*Ibid.*
17	W. Va.	Orchard	Sec. Mamm., Carnegie Mus., Cat. No. DC 993
31	Va.	Keyser Farm	Manson, MacCord and Griffin, Pap. Mich. Acad. Sci. Arts & Lett. 29: 375–418, 1944
32	Pa.	Rockshelter	Poole, Reading Pub. Mus. Art Gallery, Bull. 15, 1939

The opossum was utilized by the American Indian wherever it occurred. Because of its palatability and the ease with which it could be captured, it might reasonably be expected to occur in Indian refuse material if it were at all common in the area during the time a site was occupied. Skeletal remains of the opossum have been reported from at least the archeological sites in the northeastern United States listed in Table 1.

In contrast to the abundant archeological record of the prehistoric occurrence of the opossum in the Lower and Middle Ohio Valley and in Ohio north to the shore of Lake Erie, opossum remains are conspicuously absent from

TABLE 2.—*Archeological sites from which opossum remains have not been reported*

MAP NO.	STATE	SITE	REFERENCE
18	W. Va.	Globe Hill	Mayer-Oakes, W. Va. Arch. Soc. Publ., 3: 1–32, 1955
19	W. Va.	Dixon	Dragoo, unpubl. MS, Sec. of Man, Carnegie Mus.
20	Pa.	Varner	Mayer-Oakes, unpubl. MS, Sec. of Man, Carnegie Mus.
21	Pa.	Scarem	Mayer-Oakes, Pa. Arch., 24: 45–62, 1954
22	Pa.	Blairsville	Guilday, Pa. Arch., 25: 142–147, 1955
23	Pa.	Fort Hill	Gilmore, Jour. Mamm., 27: 227–234, 1946
24	Pa.	Martin	*Ibid.*
25	Pa.	Phillips	*Ibid.*
26	N.Y.	Ripley	Parker, N.Y. State Mus. Bull., 117: 459–554 ,1907
27	N.Y.	Frontenac	Ritchie, Res. Trans. N.Y. State Arch. Assn., 10 (1), 1945
28	N.Y.	Brewerton	Ritchie, *idem*, 11 (1), 1946
29	N.Y.	Robinson, Oberlander 1	Ritchie, *idem*, 9 (1), 1940
30	N.Y.	Lamoka Lake	Ritchie, *idem*, 7 (4), 1932
33	N.Y.	Staten Island	Wissler, Anthrop. Pap. Amer. Mus. Nat. Hist., 3, 1909.
34	Conn.	New Haven	MacCurdy, Amer. Jour. Sci., ser. 4, 38: 511–522, 1914
35	Mass.	Cotuit Point	Wyman, Amer. Nat., 1: 561–584, 1868

Indian sites in northern West Virginia, southwestern Pennsylvania, and central New York State. The archeological sites listed in Table 2, all with associated mammal faunas and all from within the present range of the animal, agree in the absence of opossum remains.

The archeological sites listed above were not all occupied contemporaneously. They represent several different cultures and time horizons. The oldest (Nos. 4, 18, 27, 30) may be three to four thousands years old and were inhabited by pre-ceramic Archaic peoples. Sites No. 15 and 32 contained much modern refuse and these two records may well be invalid. The greatest number of them have been dated at from 1400 to 1600 A.D. (Nos. 1, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 17, 20, 21, 22, 23, 24, 25, 31). The sites on the eastern seaboard (Nos. 32, 33, 34, 35) are of unknown age but are presumably late prehistoric. All of the sites in this report date from times prior to the European settlement of the area and its attendant ecological changes. Regardless of their actual chronological position within the last three or four thousand years, they do suggest a common pattern of opossum distribution. Localities are, as yet, too few in number for an analysis by archeological time horizons to be significant, or to enable a definite northern limit to be placed on the prehistoric distribution of the opossum in North America. What the data do suggest, however, is that the opossum either did not occur or was a rare mammal in the Appalachian Plateau of northern West Virginia, western Pennsylvania and southern New York State.

This distributional picture is admittedly incomplete and must await the further activities of the archeologist for its completion. It does, however, agree with the historical evidence for the late migration of the opossum into more northerly regions.

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OBSERVATIONS ON A POPULATION OF SMALL MARSUPIALS IN TASMANIA

By Eric R. Guiler

The marsupial fauna of Tasmania is well known from the taxonomic standpoint, and the geographical range of the species both in Tasmania and on the mainland of Australia is also known in some detail. However, the distribution of many of the marsupials within Tasmania is very imperfectly understood and there are many pressing problems in this regard yet to be solved.

There has never been any attempt to investigate either the movements of individual animals or the microdistribution of one or more species in any one area of Tasmania. As far as I am aware the work being carried out at Canberra by Dunnet of C.S.I.R.O. is the only attempt at such studies in the southern or eastern States of Australia. The macrodistribution of several of our Tasmanian species has been worked out in more or less detail. The distribution of the brush possum, *Trichosurus vulpecula*, was described by Pearson (1938), Huxley (1938, 1942), and more recently by Guiler (1953) and Guiler and Ingram (1958). In all of these investigations the raw material on which the distribution curves were based was derived from fur industry statistics.

The present survey is concerned with the microdistribution and movements of individuals of two species of small marsupials in a restricted area of Tasmania on the outskirts of Hobart. Several other species are found in the same area but they are outside the scope of the present investigation.

The area chosen occupies about 80 acres on the top of a ridge to the south of Hobart in the suburb of Lower Sandy Bay. The area is native bush and it has the advantage of being located only 3 miles from the University and only 800 yards from my home. The whole area lies in one property owned by J. H. E. Dorney who very kindly allowed me to trap on his land.

The bush on the western side of the area extends up to Mount Wellington. This bush is only broken by two roads and there is very little cultivated ground. Beyond Mount Wellington the county is undeveloped and uninhabited. It is thus possible for considerable invasions of marsupials into the area to take place. On the property there is some thick scrub, open scrub and three clearings. All these places were trapped.

The area is liberally covered by trails or paths made by animals (Plate I). In the early stages of the trapping, I put traps out in these paths and the stations were chosen in positions at which it was hoped to capture the animals using the trails. However, it was found that on certain well-defined paths, as at Stations 59–62, there were few animals captured. The infrequency with which captures were made at stations situated on trails leads to the conclusion that the trails are made by the animals moving from one feeding area to another or in transit from a daytime resting place to a feeding area. In either case, it is likely that the animals do not feed very much while on the move.

The trails are very numerous, as many as five being found in one meter square, and for this reason no attempt was made to chart the trails of the area.

MAMMALS IN THE AREA

The area is populated by six species of marsupial, one species of monotreme and three species of placental mammals. The two marsupials which were investigated are the potoroo and the short-nosed bandicoot.

The nomenclature used throughout for the marsupials is that proposed by Iredale and Troughton (1934). The rodents are named following Wood-Jones (1924) and Tate (1951). The term "possum" is used to distinguish the Australian phalangers from the American didelphids. The author of each species is cited only once.

Potorous tridactylus apicalis (Gould).—This animal (Plate I), known as the long-nosed rat kangaroo or potoroo, is common in the bush around many parts of Hobart. Many people refer to this species as a bush rat, though the animal is larger than a rat.

The fur of the species is straight and soft, the soft nature of the fur making it very easy to distinguish young individuals of this species from *Isoodon*.

The Tasmanian potoroos are considered to be a geographical race separated from the mainland species by minor cranial and dental features. Wood-Jones (1924) records a white tip on the tails of the South Australian potoroos. The Tasmanian animals may or may not have a white tip on the tail. In the 41 specimens of this species which were examined, 6 had no white tip to the tail while the remainder had a tip which varied considerably in length in different individuals.

The animals do not gallop in the fashion described by Troughton (1942) but move in a typical macropod method which is surprising on account of the unbalanced appearance which it gives to the animal. The body is held horizontally and close to the ground, yet progression is achieved by kangaroo-like bounds. I have not seen them use their forefeet when moving quickly, though they use them when moving slowly. They do not move very fast but proceed in an irregular, rather zigzag course, except when following a track. Each bound takes the animal forward about 30–45 cms.

The species is strictly nocturnal and I have never put one up in the daytime. They do not come out at twilight but wait until darkness has fallen.

The animals dig small irregular holes in the ground or vegetation when feeding. These holes are not round like those made by bandicoots. They use their hands extensively in feeding, often holding food up to the mouth.

The only noises made by potoroos are a hissing noise when annoyed, and a grunt made by the males when handled. Old males made more noise when being handled than either young animals or females. Females with pouch young resist marking more vigorously than other individuals. The young ones squeak and hiss, often using a cry which is a call to the mother. Potoroos have very little fear of man and show only slight agitation on being handled.

Potoroos can be held during marking by several methods. The animals are easily lifted by the tail but to keep them still, it usually is necessary to grasp them firmly by the shoulders and the haunches or to hold them on their sides in a "foetal" position. In one case a female potoroo objected to being handled and made a great noise about it, struggling considerably. Making a noise obviously cost the creature much effort and this, combined with her struggle, causes her to faint. She recovered in about two minutes and then rapidly hopped away.

Wood-Jones (1924) noted that foxes have greatly reduced the numbers of this species on the mainland. The absence of foxes from Tasmania has undoubtedly been of advantage to the potoroo.

Isoodon obesulus (Shaw and Nodder).—In the area investigated, the short-nosed bandicoot is less common than the potoroo. As noted above, this species can readily be separated from the potoroo by the nature of the fur which in *Isoodon* is coarse with many bristle hairs. The bandicoots are smaller and more active than the potoroos and they are not so willing to approach man. In the traps they hop about and attempt more actively to escape than do the potoroos and they struggle more vigorously during marking operations. It is inadvisable to hold these animals by the tail during marking as the tail is more slippery than that of the potoroo, but the other two methods of grasping the potoroo, as described above, can be used for holding *Isoodon*.

These animals make the same kinds of noises as the potoroos.

In movements the forefeet, in contrast to those of potoroos, are always used; in slow movement these animals progress in a weasel-like manner and when running quickly they do not bound like *Potorous*. *Isoodon* cannot run as quickly as *Potorous*.

Other species.—Individuals of both species of possum occurring in Tasmania are found living in trees in the area. The ringtail possum, *Pseudochirus convolutor* (Oken) is more common than the brush possum, *Trichosurus vulpecula* (Kerr). I have seen several *Pseudochirus* in the trees but the only evidence that there are brush possums in the area is the presence of fresh scats.

The native cat, *Dasyurus quoll* (Zimmerman), also occurs in the area. I have not trapped any individuals of this species so it is not possible to decide if there is a permanent population living in the area. Dorney has seen several native cats at one time coming to a window in his home and he tells me that at one period there were in the area two families of *Dasyurus* which used to feed on scraps near his house. One native cat was killed on the road near the area in March, 1954.

Trapping failed to reveal the presence of any of the smaller marsupials in the area. This does not rule out the possibility of marsupial mice being present, especially since an adult male *Antechinus swainsonii* (Waterhouse) was caught by a cat in a nearby garden on 27 July 1950.

The echidna, *Tachyglossus setosus* (Geoffroy), also occurs in the area. The species is not numerous, only one individual having been seen, though there are many excavations made by these animals.

The barred bandicoot, *Perameles gunnii* (Gray), is found in the open paddock to the west of the area, spending the day among blackberry bushes. Only one individual of this species was caught in the trapping area.

PLATE I

TOP: An animal trail in the trapping area. BOTTOM: *Potorous tridactylus* in a trap.

The European rabbit, *Oryctolagus cuniculus* (Linn.), is thinly distributed throughout the area and nowhere does it reach pest dimensions. As far as I

PLATE II

TOP: Holes in the ground made by *Isoodon* while feeding. BOTTOM: A nest made by a potoroo.

can ascertain, the rabbit does not provide direct food competition with the marsupials of the area. Indirectly, the rabbits, especially if they are present in pest dimensions, could affect the numbers of marsupials. It was noted that in places where rabbit dung is deposited the marsupials do not dig for food so that if the rabbit became numerous, the feeding activities of the marsupials would be upset. The rabbits increased during the summer of 1954 but moderate winter hunting keeps them under control. The rabbit population is mainly surface-dwelling. One rabbit was noted by Dorney to be suffering from myxomatosis.

A species of the genus *Rattus* was caught at Station 34 on 4 August 1954. This species is probably of the *assimilis* group. Another species of *Rattus, R. lutreolus velutinus* (Thomas), was caught at Station 30. The specimen was released but has not been recaptured.

METHODS

The area was reconnoitered using a large-scale aerial photograph and by walks over the ground. Trap stations were selected usually on or near game tracks or feeding areas. The traps were baited in the late afternoon and examined in the morning, when any animals caught were either marked or their number noted.

The traps used were ordinary wire rat traps with a door closed by a spring. The traps are cheap, easily obtainable and serve the purpose efficiently but have the disadvantage that they are difficult to carry and store. Each trap was numbered so that a check could be carried out after trapping. In the later stages of the work, trial trapping was carried out using Longworth traps. Unfortunately, these were not successful.

In the initial stages of the experiment ear tags were used to identify the animals. The type of tag used was developed by A. G. Lyne, who experimented with fish fin tags which were fixed to the ears of captive *Potorous*. The tags used in the present survey were made from l-gauge aluminum pointed at one end and drilled at the other. The tags were numbered and were carried flat. In the field they were folded as necessary before attachment to the ear of the animal.

The animals were marked in the field and for this purpose they were placed in an empty sugar bag. The ear was always pierced by the tag as near the base as possible, but in spite of this precaution, nearly all the tags were torn out of the ears after one month.

During the tagging process every effort was made to avoid handling the animals more than necessary. Because of this, no body measurements were made. If the animal was not held firmly enough it usually struggled so much that large handfulls of fur were torn out of its skin. The tagging was carried out at the station at which the animal was caught and at the conclusion of this process the animal was immediately released.

It was noted that the animals did not object to having their tails handled and measurements were made of the length of the white tip, if present. This infor-

mation was most useful in the re-identification of animals which had lost their tags. Care has to be exercised that the end of the tail is clean. If the tail is fouled with excreta the white tip is not obvious and may not be noted.

When it was found that ear tags were unsuccessful, due to their being torn by fighting, tattooing was substituted for tagging.

A veterinary tattooing kit was used and the animals' ears were marked with numbers and a serial letter. The tattooing method was very satisfactory, only one animal being recaptured with an undecipherable tattoo. The disadvantage of the method is that it is not possible to carry out the operation without assistance.

Dunnett is using colored disks attached to the ears of *Trichosurus*. This method enables the animals to be identified at a distance. These is no advantage in using similar tags on either *Potorous* or *Isoodon* since these species live in thick scrub and cannot be seen at night.

I considered using the technique employed by Godfrey (1954) whereby radioactive cobalt (Co^{60}) is attached to the leg of the animal which it is desired to trace. The investigator uses a Geiger counter to find the animal. The method was not used because the maximum range at which the animal carrying the Co^{60} can be picked up is about 10 meters. The potoroo may cover a considerable distance in a night and good deal of time could be spent by the investigator without gaining much information. Furthermore, if Co^{60} were used on a number of individuals there would be no means of identifying the particular individual which was being traced by the counter.

The present investigation fell into three phases. During the first two phases, when both ear tags and tattooing were used, the traps were laid at stations over the whole area to sample the population and to record the movements of individuals. The final phase was when all the traps were set in small areas using a saturation technique to trap all the animals in the area. Two areas were "saturated," one each on the nights of 18 and 20 September 1954.

The bait used in the first two phases of the experiment was nearly always apple though fat was used on a few occasions. It was known previous to the experiment that apples were eaten by both species and this bait was used without change to avoid the food preference factor. Mutton fat was used in August, 1954, and some initial success obtained in catching *Isoodon* but further use of fat failed to take any of this species. Fat, apple and carrot were used in the final phase of the experiment.

One-third of an apple or a 1-cm.-thick slice of large carrot was used as bait. The core of the apple was always pierced with the bait hook. No bait was used twice and no uneaten baits were left in the area.

RESULTS

Trapping was done on 23 nights, representing each month except April, June, November and December, from 23 September 1953 to 20 September 1954 on the area near Hobart. Thirty traps, set at 30 different stations, were the most

operated at any one time. Apples were used for bait, supplemented occasionally by fat or sliced carrot. Animals were taken at 50 different stations and included the following numbers, exclusive of recaptures: *Potorous*, 43; *Isoodon*, 9; *Perameles*, 1; and *Rattus*, 1.

An analysis of the data shows that the *Potorous* captured included 25 males (two of them juveniles) and 18 females (two juveniles). Eighteen males were recaptured, from 1 to 5 times (average 2.5); and nine females were recaptured, from 1 to 6 times (average 2.2). Thirteen of the adult females were carrying pouch young, one in each case. The *Isoodon* included 5 males and 4 females, all adults. Only two males were recaptured, one once and the other twice. None of the females were carrying young. The one *Perameles* captured was an adult male, and it was taken only once.

DISTRIBUTION OF THE SPECIES

Perameles gunnii.—It is recognized generally that the barred bandicoot is a dweller in open country, living by day in grass tussocks or under bushes and coming out at night to feed. This generality is supported by *Perameles* being trapped in the open paddocks to the west of the area (Station 1) and in the cleared barrack area. On no occasion has this species been seen or trapped in the wooded portions of the area investigated, or in the surrounding country.

Potorous tridactylus.—The potoroo has been caught over all of the area, both in open country and the scrub. The habitat of the species thus ranges from the thick scrub through open woodland to the cleared areas. It does not appear to wander into the extralimital paddocks on the western boundary of the area. The nature of the substratum does not appear to influence the distribution of the species since these animals were trapped on rocky ground as well as on *Casuarina* needles and grass. It is noticeable, however, that the animals progress very much less rapidly and safely over the rocky ground, a factor which would be important if predators were active in the area.

The potoroo, although found over all of the area, shows a very definite preference of habitat. Analysis of the animal histories in relation to the distribution of the vegetation shows that of the 96 potoroo captures, 59 were made in thick scrub or at stations close to thick scrub, 18 in open scrub and 19 in open areas.

Allowing for the fact that a trap placed up to 5 yards from thick scrub would attract an animal out of that scrub, approximately 40 per cent of the *Potorous* captures were made in either open areas or in open scrub. There are two possible explanations for these captures. The first is that these animals may have been feeding in the more open areas but this is unlikely because there are very few scratchings in these areas. The second explanation is the more likely, namely that the animals were captured while in transit from one feeding area to another. Most of the captures in open areas were made in the spring when the population was in the most nomadic phase.

Isoodon obesulus.—Individuals of this species have been trapped in the two

large open areas (Stations 1, 2, 23) as well as in thick scrub at Stations 57 and 67. Only nine specimens of this species were caught during this investigation. It is possible that the species is more wary than *Potorous*, or else it does not like apples, or there are not many of them in the area. I am inclined to believe, on very slight evidence, that there are more of them present in the trapping area than the results indicate and that they dislike the apple or fat baits offered, since the bait is often left only partly eaten.

It is significant that all but four of the animals taken were males, indicating that the females are more wary than the males or else fewer in the population.

Reference to the station histories shows that traps were set 120 times at stations where *Isoodon* had previously been caught, yet only 12 animals were captured.

From the above results it is possible to indicate the ecological habitats occupied by the small ground-feeding marsupials. *Perameles* favors open plains, paddocks and cleared areas; *Isoodon* open timbered country but overlapping into thick scrub; and *Potorous* occurs in thick scrub and possibly forests. Kershaw (1946) has noted the presence of the bettong, *Bettongia cuniculus*, at the edges of forests. This species does not occur in the area examined.

It is worthy of note that a possible gradient of physical activity exists which can be correlated with the above habits. The potoroo is much less active in the trap than *Isoodon*, which in turn is less active than *Perameles*, indicating that species living in open country are more active than those in the scrub. I am not sufficiently familiar with the habits of the bettong to draw any conclusions relating to the physical activity.

The potoroo is a much more heavily built animal than either of the bandicoots which is in accordance with expectations of a scrub-dwelling species. However, the bettong is much larger than a potoroo.

DISTRIBUTION OF INDIVIDUALS

Potorous.—For the purpose of this survey the animals caught can be divided into four categories, namely: (*a*) Those caught four or more times, (*b*) those caught three times, (*c*) those caught twice, and (*d*) those caught only once. The animals of categories *c* and *d* give no information as to movements of individuals in the population. The movements of individuals in relaton to time shows that there is a period of general unrest during the spring, when the animals move restlessly around the area. This is especially true of the males. During most of the remainder of the year, the individuals of the population adopt a number of temporary home ranges and can be trapped at any of several stations a short distance apart during a brief period.

The home range is not occupied as a permanent range throughout the life of the individual. Animals which have been caught on several occasions in one area have been taken three months later in another area in which they apparently had resettled themselves.

In the later stages of trapping (May to September, 1954) only a few of the

original population were recaptured. The potoroos, therefore, are seminomadic in habit.

The males, in the spring breeding season, move very considerably over a wide area. This movement is apparently continuous, there being no settlement into temporary home ranges. Animals have been taken on successive nights at the opposite end of the trapping area from that in which they were originally taken. The movement of any one individual male may cross the track of one or more males, thus indicating that there may be no territory claimed by individual males even during the breeding season.

During the spring, the females also move considerably but these movements are not as wide in extent as those of the male. Again there seems to be no territory occupied.

Isoodon.—Animals of this species were recaptured so infrequently that no conclusions can be drawn regarding the movements of individuals. One particular migration is of interest. Animal No. 31 was taken about half a mile away from the station at which it was captured (Station 23). It was tattooed at this place and escaped immediately afterward. One month later it was recaptured at a station adjoining that at which it was originally captured. This may be coincidence as six months later it was caught at Station 34, about 300 yards away from Station 23.

TOTAL POPULATION

In the early stages of the experiment, it was hoped to estimate the total population of the area using recapture data as a means of calculation. Examination of the literature of population estimates revealed that other workers, e.g., Jackson (1939) and Bailey (1952), used large samples on which to base their calculations. On advice from Mr. Sprent of the Mathematics Department of the University of Tasmania, it was decided that little would be gained by applying their methods to the present sample. The method used to estimate the total population is that of Green and Evans (1940) as described in Allee *et al.* (1949) and Dice (1952). These authors used the "Lincoln Index" as a means of estimation. For the purpose of this survey the period to October 4 is taken as the precensus period in which 16 animals were marked. The period October 28–31, the census period, saw 8 new potoroos captured and 17 recaptured. Of these 17, 6 were caught twice, leaving 11 as the recapture number.

Therefore, the number of nontagged potoroos present in the precensus period $= 16 \times 8/11 = 12$. The total number of potoroos present $= 12 + 16 = 28$.

The population of *Isoodon* is more difficult to estimate because of the lack of satisfactory recapture data. However, assuming the precensus period to be up to October 3, and the census period up to May, 1954, the total population of *Isoodon* is 8 individuals, giving a grand total of 36 for the two species.

However, with the continuance of the project a total of 40 *Potorous* and 9 *Isoodon* were marked and in the later stages of the investigation very few recaptures were being made. It would appear that either the previously

captured animals were very trap-conscious, or else the composition of the population changed almost completely. Negative trap-consciousness certainly did develop but I find it hard to believe that it could occur among such a large number of animals, each with a different amount of trap experience. It is more likely that the population changed and this makes unreliable any estimates of population density over a long period. In any future work, it is recommended that short-term trapping be used for population estimates.

It has been stated above that *Potorous* is very selective in its choice of habitat and the total area occupied by this species is not greater than 25 acres, giving a population density, based on short-term estimates for this species, of about 1 per acre. In certain areas, e.g., Stations 26–29, the density of population is much greater than this, about 10 individuals occupying an area of 2,500 square yards.

Local dense populations such as this have been noted in the field in other localities. At Stewart's Bay, near Port Arthur in southeastern Tasmania, five individuals were operating in an area of 5,000 square yards, a density of nearly 5 per acre.

GENERAL

During the course of this investigation, several points of interest on the biology of the species have appeared as incidental matters. Some individuals showed not only a white tip to the tail, but also had the end of the tail either naked, unpigmented or both.

The *Potorous* population was largely dominated by males, there being 24 males to 17 females recorded from the area. It is possible that the females are more wary than the males and do not enter the traps so freely. There is some evidence for this in the analysis of the number of captures of each sex. Males were taken 71 times and females only 37 times. The females were thus caught fewer times than might be expected from the ratio of males to females as caught. On the other hand, these figures may indicate that the males show greater activity than the females. In this connection it is interesting to divide the year into three-month periods as set out in Table 1, each period corresponding to the phases of sexual activity in the species.

TABLE 1.—*Potorous captures in relation to the sexual cycle*

	AUGUST–OCTOBER SPRING, BREEDING	NOVEMBER–JANUARY SUMMER, NON-BREEDING	FEBRUARY–APRIL AUTUMN, BREEDING	MAY–JULY WINTER, NON-BREEDING
No. of captures plus recaptures	30+17	12+7	28+8	4+2
No. of trapnights	235	32	167	63
No. of captures per trapnight	0.2	0.6	0.2	0.09

These figures show that the greatest amount of that particular activity which leads to the capture of a potoroo occurs during the summer period. This activity is probably feeding. During the winter the feeding activity falls off considerably or else it changes in its form, the animals moving from one type of food to another, this change resulting in fewer animals being trapped. During the breeding seasons the catch per trapnight is lower than in the summer period.

Neither Asdell (1946), Wood-Jones (1924) nor Zuckerman (1953) give any information of the breeding season of the potoroo. Although the sample considered in this study is small, some useful information on breeding has been gathered.

Only one pouch young is carried at a time and it remains in the pouch until some time after it is furred. Very small young (less than 4 cm. crown-rump length) were noted in January, May and September. Large, well-furred specimens were found in October and February. Juvenile animals were trapped in September and March.

From the above it can be concluded that there probably are two breeding seasons in the year at which the females become pregnant, though some breeding apparently takes place throughout the year. The first season is in the early spring, late August to early October, the young being found in the pouch in late September to November with the juvenile potoroos joining the population as free-living individuals in February of the following year.

The second season, a period of lesser activity, takes place in January with young in the pouch in that month and also in February. These young join the adult population in September or November of the same year. I do not know if females pregnant in January or September, and therefore carrying young in September or January, mate and become pregnant in September or January.

Females which were carrying young other than during the normal breeding season may have been animals whose normal pregnancy or lactation had been interrupted. However, the behavior of Animal No. 18 provides some evidence against this view. This animal, when captured on 30 October 1953, dropped a well-developed but unfurred young after release. When recaptured on November 1 she had no young in the pouch so it can be assumed that she lost the baby. When again captured on 26 February 1954, she had a small (4.5 cm. C.R.) young in the pouch. It would appear that she had not come into oestrous until the next season, January–February.

Copulation has not been observed and it is not known whether delayed implantation of the blastocyst takes place, as has been observed in other macropods (Sharman, 1954). Sharman found that the wallaby *Setonix* experiences 28-day oestrous cycles during the period from late January to the end of October, with a summer period of anoestrous. He found that in nature *Setonix* breeds only once per annum. It is thus within reason to expect that *Potorous* is also polyoestrous, and from the evidence cited above, this would appear likely. *Potorous* differs from *Setonix* in that there are two breeding seasons per annum.

The female carrying a pouch young in May (Animal No. 52) is an interesting case. The mother was a small animal and this was probably her first baby. It is possible that she reached puberty and came into oestrous at a time out of phase with the cycle of the majority of the population.

Potorous mothers take little care of their young. In two cases a large furred young which fell out of the pouch was replaced by me but was dropped by the mother as she ran away. It is difficult to decide whether the young was dropped deliberately by the mother or as a result of the effort of running. It should be emphasized that I have only seen large young (more than 5 cm. C.R.) being dropped from the pouch. The mother can close the entrance to the pouch by muscular action and it requires some force to open the aperture against her will. In view of this it appears that she may drop the young deliberately.

Both *Potorous* and *Isoodon* feed in certain regions. The location of these regions changes from time to time as can be seen from the distribution of scratching over the trapping areas. The region around Stations No. 27–33 appears to be in almost constant use as a feeding site but much of the rest of the trapping area is only used at irregular intervals. The gulley region is used by a large number of animals, probably a total of 10 of both species, whereas the other areas are used by far fewer individuals.

The animals use well-defined trails when traveling from one feeding site to another. Individuals feed in regions within a loosely established home range. After a time, the individuals appear to move to other home ranges nearby, based on different feeding regions. The extent of the movement is not known, though it may not be great since extralimital trapping failed to catch any marked individuals.

The potoroo has been recorded as building a nest (Kershaw, 1946). The nest is constructed of dry grass with no definite structure but is hollow within (Plate II). I have never flushed a potoroo out of a nest in the daytime and I have only found nests which are old or unoccupied. It may be that the nests are only constructed at the breeding time by females. Only one animal attempted to construct a nest in a trap and this was a pregnant female which was later found with a young in the pouch (Animal No. 7).

Careful searching of the area showed that little information can be gained from the scatology of the area. The feces of dogs were commonly seen but the scats of larger marsupials were never found. The feces of both *Potorous* and *Isoodon* are small in size and almost identical in appearance. It would be impossible to distinguish them in the field and the scats are so small that they are concealed by grass and undergrowth, thus making impossible any attempt to estimate the population from the number of scats. In the course of the field work, only one group of scats (*Potorous* or *Isoodon*) was observed. It may be possible to estimate the population of the open-country population of *Perameles* by a method similar to that used by MacLulich (1937), who correlated the number of hares in one area with the number of scats encountered on a standard walk.

Scats of the ringtail possum, *Pseudocheirus convolutor*, were noted at the bottom of trees inhabited by this species and scats of the brush possum, *Trichosurus vulpecula*, were found on two occasions near discharged but empty traps.

SUMMARY

Live-trapping experiments were carried out to investigate the movements and distribution of a population of *Potorous tridactylus* (Gould) and *Isoodon obesulus* (Shaw and Nodder). The animals were caught in cage-type rat traps and were marked by either ear-tagging or tattooing. The first method was found unsatisfactory. In spite of precautions, it seems likely that a negative trap-consciousness was built up and it is recommended that, in future, intensive trapping be carried out over a short period.

Potorous occurs mainly in thick scrub though it ranges considerably. Insufficient captures were made of *Isoodon* to draw definite conclusions as to its habitat. Traps set on game trails did not yield many captures, feeding areas being more lucrative.

During the spring the population is restless, especially the males. The animals move around the area. During the rest of the year the animals adopt a number of temporary home ranges. Certain feeding areas are always used, though the individuals captured there differ from time to time.

The total number of *Potorous* present was calculated as 28, though it is doubtful that this information is of much value in view of the semi-nomadic nature of the species. In the later stages of the work it was found that the population was almost entirely new, this pointing to a movement of the original population to some new area.

The population of *Potorous* was dominated by males, which were caught more frequently than females.

The presence of pouch young with the females showed that there are two breeding seasons in a year, one in the spring and the other in the mid- or late summer.

The small size of the scats makes it impractical to carry out any investigation of the scatology of the species.

ACKNOWLEDGMENTS

I am greatly indebted to Mr. J. H. E. Dorney, not only for permission to trap on his property but also for assistance with the trapping. I was assisted in the tagging by a number of people to all of whom I am very grateful. In this connection I must especially mention Mr. I. Rowley of C.S.I.R.O., Wildlife Section; Mr. Peter Roberts; Dr. H. C. Reynolds of the University of California; and my wife. I am indebted to Dr. K. G. Meldrum of the Tasmanian Department of Agriculture for the loan of the tattooing kit. The Tasmanian Animals and Birds Protection Board kindly granted me a permit to undertake this work. Professor V. V. Hickman kindly checked the typescript of this paper and made many helpful suggestions. I am grateful to Dr. Ralph W. Dexter for his assistance in the final preparation of the paper and in reading the proofs.

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RUDIMENTARY MANDIBULAR TEETH OF *SCALOPUS AQUATICUS*

BY CLINTON CONAWAY AND STUART O. LANDRY, JR.

The dental formula usually given for the prairie mole, *Scalopus aquaticus*, is:

$$\frac{3}{2}\,\frac{1}{0}\,\frac{3}{3}\,\frac{3}{3} = 36$$

This formula dates from Mivart (1867) and Dobson (1882) and has been more or less uncritically accepted since that time. However, it was early noted that in the lower jaw, small rudimentary teeth sometimes appear in the gap between the incisors and the premolars. Mivart (1867) noted that in one

British Museum specimen a minute rudimentary tooth was found which he thought might represent the canine.

Leche (1895) sectioned the head of a juvenile *Scalopus*, 49 mm. in length from nose to anus, and described the development of the milk and permanent dentition. He noted that posterior to I_2 a third tooth appeared that was represented by both milk and permanent primordia. He called these "dI_3" and "I_3." The primordium of the milk tooth was well developed but that of the permanent tooth was degenerate. In addition to these primordia, Leche found another pair which he called "dC" and "C." He described them as perfectly formed and noted that in his specimen, the permanent one was calcified but undergoing resorption. He stated that "C" often develops into a small peg-like tooth that may be found in adult moles. Leche gave the following complete dental formula for *Scalopus*:

	I:	C:	P:	M:	
Upper jaw	1 2 3 1 2 3	1 1	2 3 4 2 3 4	1 2 3	
Lower jaw	1 2 3 1 2 3*	1 1*	2 3 4 2 3 4	1 2 3	

Large numbers designate permanent teeth; small numbers, milk teeth. Asterisks indicate the abortive teeth in the series. Leche recognized that the assumption that the first abortive tooth is an incisor and the second a canine was unwarranted but stated that he adopted Dobson's formula as a point of departure.

Jackson (1915) stated in a footnote (p. 30), "The actual dentition of *Scalopus* is: i.3/3; c.1/1; pm.3/3; m.3/3; total, 40. The third lower incisor and the lower canine are non-persistent and disappear before the animal is mature." This would indicate that teeth at both of the sites "I_3" and "C" temporarily persist. We have confirmed that two teeth may appear in the gap between the incisors and premolars (Plate I, 3–4) although more frequently only one occurs.

The question then arises whether these two rudimentary teeth are: (1) Milk and permanent representatives of the same tooth, (2) milk "I_3" and "C", (3) permanent "I_3" and "C", or (4) the milk representative of one and the permanent of the other, as implied by Leche in stating the permanent "I_3" was degenerate while permanent "C" persisted.

The purpose of this paper is to call attention to the fact that either or both of these two rudimentary teeth may persist in adult moles and to describe the enamel organs of these teeth in sections of the heads of juvenile moles to determine which of the above four explanations is correct. Our secondary purpose is to describe differences in the frequency of occurrence of the rudimentary teeth between populations from different parts of the range of *Scalopus*.

MATERIALS AND RESULTS

The senior author collected a series of *Scalopus* near Madison, Wisconsin, from which 439 mandibles were available for study. In this series rudimentary

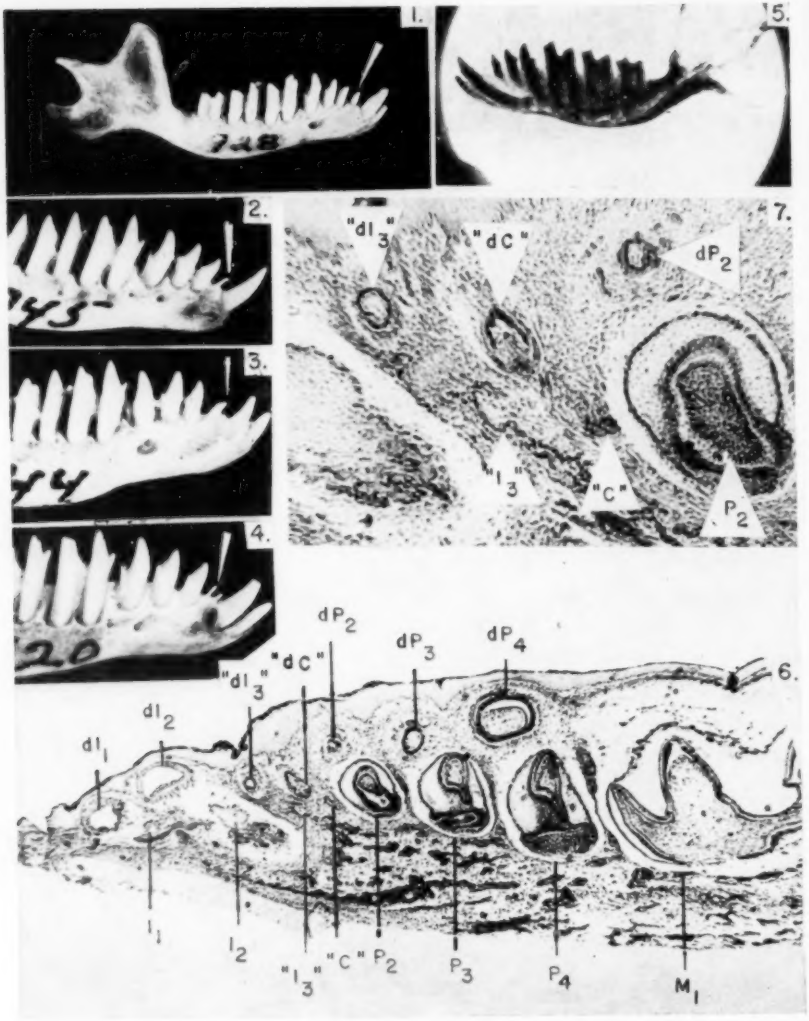

PLATE I

1, *Scalopus* mandible with single large diastemal tooth indicated by arrow. 2, Mandible with single spicule indicated by arrow. 3, Mandible with two spicules; the posterior spicule is indicated by the arrow; the minute spicule immedately anterior to this is difficult to distinguish. 4, Mandible with two spicules; the posterior spicule is indicated by the arrow. 5, Cleared mandible showing procumbent root of the second incisor. 6, Photomicrograph of anterior portion of mandible of 58-mm. nestling; the teeth and primordia are indicated. 7, Enlarged section of 6; note the degenerating permanent primordia of the rudimentary teeth.

teeth in the lower jaw diastema are more common than in any other series that we have examined. Consequently, most of the following remarks refer to observations on these specimens. We have, in addition, examined mole jaws from other localities, as listed in Table 1. The occurrence of rudimentary teeth in moles from these areas is described below.

Gross appearance.—The form of the rudimentary teeth is quite variable. Often, there is only a hole in the surface of the dentary through which protrudes a lump of enamel. The tooth in this form usually escapes notice because museum cleaning procedures usually do not remove a strip of gum tissue lying over the dentary in the diastema.

Another common variation is a single small spicule lying just in front of the first functional premolar (usually designated P_2; Plate I, 2). This spicule may be almost invisible to the naked eye; it may be quite conspicuous; or in a very few cases it may be actually functional, as in Conaway 728 (Plate I, 1).

Two rudimentary teeth were found in eight mandibles. In six of these, both teeth were small spicules (Plate I, 4) and in two the posterior tooth was large and the anterior much smaller (Plate I, 3). These eight specimens do not indicate which of the four identifications of the rudimentary teeth mentioned above is correct.

We also examined the cleaned jaws of some very young nestling animals. Much gum tissue containing milk teeth remains in place on these specimens. In University of Kansas 1703, right jaw for example, milk P_2 is clearly in place above P_2. Although there are teeth in the diastema between the incisors and premolars, one cannot safely say whether the teeth are milk or permanent or whether both dentitions are present. It is too easy to confuse bits of connective tissue with teeth, even after clearing the mandibles in oil of wintergreen.

Microscopic appearance.—Mandibular serial sections were prepared from two fetuses of 36 and 41 mm. length (nose to anus) and from five nestling

TABLE 1.—*Frequency of occurrence of rudimentary teeth in Scalopus populations*

GEOGRAPHIC LOCATION	ADULT MANDIBLES		JUVENILE MANDIBLES	
	No rudimentary: rudimentary	Per cent with rudimentary teeth	No rudimentary: rudimentary	Per cent with rudimentary teeth
Wisconsin	243:82	25	36:78	68
Indiana	69:5	7		
Missouri	131:21	14	52:8	13
Western Kansas	27:11	29	21:15	42
Eastern Kansas	63:6	9	20:34	63
Minnesota	9:3	25	1:1	50
New York	51:3	6	24:0	0
N. and S. Carolina, Georgia, Flordia	51:1	2	6:0	0
Arkansas, Louisiana, Texas	48:4	8	18:0	0
Massachusetts	39:5	11	27:15	36

young of 45, 48 and 58 (three specimens) mm. length. Two deciduous teeth between dI_2 and dP_2 are found in each of the specimens. These teeth seem to develop somewhat more slowly than the remaining lacteal teeth. Enamel is not yet present in the rudimentary deciduous teeth of the fetal specimens while the remaining deciduous teeth have an enamel deposit. A corresponding lag in development is seen in the nestling young although enamel is deposited in all deciduous teeth.

Two minute structures which appear to be the tooth germs of the permanent rudimentary teeth are visible in the fetal specimens and in the smaller nestling animals. Germs of the permanent rudimentary teeth can be seen clearly only in the three 58 mm. nestling specimens (Plate I, 6–7). These germs are vestigial and degenerating. They appear as unorganized masses of cells with pyknotic nuclei. We interpret this as evidence that the permanent rudimentary teeth do not form. Therefore, the rudimentary teeth seen in the adult jaws are considered to be retained lacteal teeth.

Frequency of occurrence.—The frequency of occurrence of rudimentary teeth was tabulated in samples of populations from various parts of the range of *Scalopus* (Table 1). Any enamel structure between dI_2 and dP_2 was recorded as a rudimentary tooth. The specimens were separated into juvenile and adult categories by determining the extent of tooth wear. Juveniles are defined as animals taken between the time of entry into the population in late spring and December 31 of that year. All other specimens are classed as adults.

Although the samples are small, it is apparent that the ratios of animals with rudimentary teeth to those without rudimentary teeth vary over the geographic range in both juveniles and adults. A chi-square test for independence gives highly significant results ($P = .01$) for both groups of ratios.

The data further suggests that in general rudimentary teeth occur with the highest frequency in the northwestern portion of the range and that the frequency decreases in a north-south cline and a west-east cline. The data were judged insufficient to warrant statistical analysis of this distribution.

DISCUSSION

The above evidence suggests that the rudimentary teeth in *Scalopus* are usually retained milk teeth. Retention of milk teeth in *Talpa* has been noted by Woodward (1896) and Sicher (1917) and in *Parascalops* by Eadie (1944). Possibly a tooth of the permanent series may develop occasionally in the diastema of *Scalopus* since in four mandibles a single, well-developed, and apparently functional tooth occurs in this position. The tooth is much wider and higher-crowned than the spicules usually found in the diastema. Microscopic study of a few fetal specimens cannot clarify this point if development of a permanent tooth occurs only rarely.

A factor in mandibular tooth number reduction in *Scalopus* is the characteristic hypertrophy of I_2. Plate I, 5 shows a cleared mandible in which the procumbent permanent I_2 extends into the mandible beneath the premolars to the base

of P_4. Some of the anterior mandibular teeth fail to form since there is little space for their roots to develop. Formation of most of the anterior milk teeth can occur since dI_2 is relatively shallow-rooted. Ordinarily the massive root of the permanent I_2 preempts the space where the larger and deeper permanent primordia would develop in the diastemal region. One tooth of the primitive eutherian series (usually identified as P_1) is not represented by either deciduous or permanent primordia. Presumably this tooth has been completely lost through the hypertrophy of I_2.

The evidence suggests that when only one rudimentary tooth is found it develops from the posterior diastemal primordium. The posterior milk primordium is better developed than the anterior in the seven fetal and nestling specimens which were sectioned. In the eight intact mandibles with two rudimentary teeth, the posterior is the larger even when both teeth are spicules (Plate I, 3–4).

As Leche (1895) stated, there is no basis for identifying the teeth of *Scalopus* in terms of the primitive eutherian dentition. Presumably a hypertrophied I_2 would encroach upon the diastemal primordia from anterior to posterior. The completely missing tooth would probably be I_3 and the two rudimentary teeth would be C and P_1. The fact that all of the teeth from the anterior rudiment to P_4 successively increase in size would support this hypothesis. We do not propose to alter the accepted dental nomenclature for *Scalopus*, however, since there is no positive evidence showing the position of the missing tooth.

The tabulation of the frequency of occurrence of rudimentary teeth shows that when sample sizes are adequate, a higher percentage of juvenile than adult animals have rudimentary teeth. This would be expected because the shallow-rooted rudimentary teeth are probably easily lost. Geographic variation in the premolar formula of *Scapanus* has been noted by Palmer (1937).

Acknowledgments.—Our thanks are due to the authorities of the following institutions for the loan of specimens: Museum of Comparative Zoology, Department of Mammals; American Museum of Natural History, Department of Mammals; University of Kansas, Museum of Natural History, Department of Mammals; Texas Cooperative Wildlife Museum, Agricultural and Mechanical College of Texas.

We are especially grateful to Dr. E. Raymond Hall of the University of Kansas Museum of Natural History for permission to section the heads of alcoholic juvenile and fetal specimens in the collections of that institution.

SUMMARY

One or two rudimentary teeth frequently persist in the mandible of *Scalopus*. These teeth are located in a diastema between the large second incisor and the premolar series and usually are retained lacteal teeth. The permanent primordia of these teeth degenerate. Apparently the large root of the second incisor exerts a crowding effect which results in suppression of these permanent primordia.

The frequency of occurrence of rudimentary teeth in populations varies with age and with geographic location. A higher proportion of juveniles than adults possesses rudimentary teeth. Populations in the northwestern part of the species' range have the highest frequency of occurrence while those in the southeastern part have the lowest.

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ECOLOGICAL OBSERVATIONS ON LASIURINE BATS IN GEORGIA

By Denny G. Constantine

During the period August 8, 1955 to June 30, 1956, while engaged in wildlife rabies investigations at the Newton Field Station, 12 miles southwest of Newton, Baker County, Georgia, the writer took advantage of occasional opportunities to seek out and observe Lasiurine bats. Time was not available to regularly investigate all potential habitats, but several thousand trees in the major habitats (Norris: Distribution and populations of summer birds in Southwestern Georgia. Univ. of Ga. Press, 1951, pp. 1–67) and in the various orchard types were explored during this period. Bats were first discovered in two areas of similar habitat type in February, and these areas were frequently visited thereafter. Thirteen bats were captured, examined, banded and released. Other bats either escaped or were left undisturbed. A total of 23 bat/day observations were made: 21 *Lasiurus seminolus*, 1 *Lasiurus b. borealis*, 1 *Dasypterus floridanus*. Some bat duplication is included and possibly more than realized. Therefore, the actual number of bats observed is not known. The use in this paper of the names *seminolus* and *floridanus* does not imply that the author is convinced of the status of these forms.

Habitat.—The two areas regularly investigated were moss-laden oak hammocks, occurring in the Dougherty Plains section of the Upper Coastal Plain of

southwestern Georgia, the climate of which is characterized by long, warm summers and short, mild winters. Average July daily temperatures range from 80.6 to 82.2°F., average January temperatures from 48.2 to 52.4°. The average dates of first killing frosts are November 9–15, last killing frosts March 10–21. The average annual precipitation is 47.67 to 51.96 inches, being well distributed throughout the year but greatest in July and August, lightest in October and November.

Oak hammock No. 1 is an area situated at the western edge of Camilla, Mitchell County, adjacent to a sewage disposal plant. The 40,000-sq.-ft. area investigated is part of a ½-sq.-mile forest almost surrounded by cleared land but barely continuous on the west and northeast with other nearly isolated forests. The area is transected by roads, trails and streams. The forest, primarily live oak, *Quercus virginiana*, has a canopy of approximately 100 ft. with a light concentration of 5 ft. underbrush, providing a theoretical vertical flight space of 5–30 ft. within the forest proper. Grown trees are generally spaced at 5–15-ft. intervals. A light odor of sewage permeates the forest, and noise of heavy machinery and autos is present throughout the day. Spanish moss grows in great concentrations on trees bordering roads, trails and streams. Six of the heavily moss-laden oaks were regularly checked for bats. Four of the six yielded bats. Other trees were examined with less regularity.

Oak hammock No. 2 is an area at the Newton Field Station situated west of Ichawaynochaway Creek and separated from the creek by a narrow strip of streambank forest (Norris, *loc. cit.*). It is bounded on the west by an unpaved road, beyond which lies an extensive pine forest. The forest canopy is generally 80–100 feet., and a sparse growth of underbrush occasionally rises 6 ft. Trees are spaced 35–75 ft. apart, theoretically correcting what might otherwise be inadequate flight space. The silence is frequently broken by motor vehicles on the road and nearby highway. Six heavily moss-laden overcup oaks, *Quercus lyrata*, within an area of about 40,000 sq. ft. were regularly checked on dates indicated below. Three yielded Seminole bats.

Oak hammocks Nos. 1 and 2 were investigated on the following dates: Feb. 8–12, 14, 15, 21–23, March 5, 22–30, April 1–9, 11–21, May 23, 24, June 2, 5, 6, 18–20. Bat/day observations for *L. seminolus* at oak hammock No. 1 are: Feb. 8 (1), 12 (1), March 5 (1), 22 (1), 23 (1), 26 (1), April 21 (3). Similar data for oak hammock No. 2 are: Feb. 21 (1), 22 (1), March 22 (1), 23 (1), 24 (1), 25 (1), 30 (1), April 1 (1), 11 (1), 19 (2), 20 (1). One *L. borealis* was found in oak hammock No. 1 on April 11, and a *D. floridanus* was discovered in that area April 3.

Moss shelters.—In every instance bats were discovered hanging in or on pendant clumps of moss. In oak hammock No. 1 bats were found in moss on four live oaks and one overcup oak. In oak hammock No. 2 they were found in moss on three overcup oaks. At the former site all bat-occupied trees formed canopies continuous with the forest canopy except on one side which formed forest edge at a road or trail. The forest canopy at oak hammock No. 2 was

open. Of 23 bat/day observations made, the following bats were in moss clumps situated on the respective sides of trees: N, 1; E, 1; S, 2; W, 5; SW, 14. Bats inhabited the interior of moss clumps excepting one Seminole bat found clinging to the north side of a moss clump on February 5 and discovered March 22 on the north side of another clump 200 ft. distant. The same observations provide the following data on elevation of hanging bats: 3½ ft., 2 bats; 6 ft., 11 bats; 9 ft., 6 bats; 15 ft., 4 bats.

Bat-inhabited moss clumps were usually shaded from the sun, but several were in full sunlight at certain times of the day. Clumps were suspended over ground covered with brown, dead leaves, providing a minimum of reflected sunlight. In no instance were limbs present beneath the moss. With one exception, the immediate flight area was considered adequate, bordering a clearing, trail or road.

Social habits.—According to the 23 bat/day observations, hanging bats were apparently strictly solitary until the latter half of April. Seventeen *Lasiurus seminolus*, one *Dasypterus floridanus* and one *Lasiurus borealis* were thus solitary, and with one exception, each was the only bat found in the respective 40,000-sq.-ft. area that day. On April 19, an apparently young male *L. seminolus* was in a moss clump 4-ft. from a clump containing an adult female bat of the same species. On April 21, two adult female Seminole bats occupied the same clump but were one foot apart. A solitary Seminole bat occupied another clump clump 200 ft. distant on the same date. Different bats occupied the same clumps on different dates. At least two, perhaps four, *L. seminolus* occupied one clump on different dates from March 22–30. Two different Seminole bats occupied the same clump on April 1 and 11, respectively. Similarly, a moss clump containing a Seminole bat on February 8 was occupied by a different Seminole bat on March 22. On March 5 a clump contained one *L. seminolus*; the same clump provided shelter for a *D. floridanus* on April 3. On March 26 a Seminole bat occupied a moss clump, which contained a *L. borealis* on April 11 and two Seminole bats on April 21. In each of the above instances there were many moss clumps in apparently identical situations in the area and on the same tree.

The bat/day per cent of total observation days each month for oak hammocks Nos. 1 and 2, respectively, were Feb., 20, 20; March, 40, 50; April, 25, 25; May, 0, 0; June, 0, 0.

Not included in the above observations are flight records of what were tentatively judged to be *L. seminolus* or *L. borealis*. These bats, flying at elevations of 20–45 ft., flew along forest edge at clearings and over roads and streams in the forest. On three evenings in February two bats flew together on what appeared to be a regular foraging route. They flew around a 200 × 200-ft. section of forest, occasionally reversing direction.

Recaptured banded bats.—Only one banded bat was subsequently rediscovered in a different site. This bat, an adult male *L. seminolus*, was found Feb. 12 hanging at an elevation of 15 ft. on the north side of a pendant clump of moss. It was rediscovered March 22 at a site 200 ft. NNW of the previous site,

hanging at an elevation of 6 ft., again on the north side of a clump of moss.

Effect of weather on activity.—Excepting for bats warmed by moss-filtered sunlight, the metabolic activity of resting *L. seminolus* and *L. borealis* seems to be dictated by the immediate air temperature, humidity, and probably air movement when the latter is present, for these species react as other heterothermic species of bats (Hock: Biol. Bull., 101: 289–299, 1951). Insufficient data regarding this subject are available for *D. floridanus*. Three Seminole bats were observed being warmed by the sun, and greatly accelerated respiratory rates indicated they must have been quite warm. Possibly the apparent preference to hang on the west and southwest exposures of trees reflects the desirability of extra heating by the sun just prior to dusk.

Captured bats were released by dropping them in the interior of a panel truck to test ability to fly immediately after hanging in shaded moss at various levels of temperature and humidity. Bats escaping capture did so by flying, thus adding to the data. Bats failing to fly after sundown also contributed to this information. Results for *L. seminolus* are presented in Fig. 1, indicating that Seminole bats are capable of immediate flight at temperatures above 70°F., possibly only at slightly higher temperature as the relative humidity is reduced, and additional data may have indicated ability to fly at temperatures lower than 70° at higher relative humidities. However, bats could not be located at such times, a development which may be worthy of further exploration. Practically no air movement was evident during these observations.

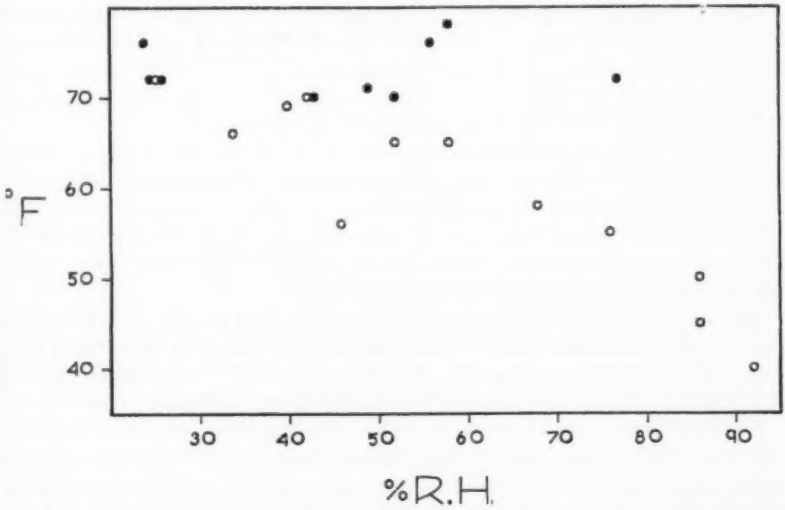

FIG. 1.—Ability of *Lasiurus seminolus* to fly at different levels of environmental temperature and relative humidity. Bats capable of flight are indicated by solid dots; inactive bats are indicated by circles.

Overlapping data suggest the occurrence of individual variation, prior disturbance, or presence or absence of "sleep." On April 19 an apparently immature male and an adult female Seminole bat were discovered occupying adjacent moss clumps, where temperature and relative humidity registered 72° and 26 per cent. The male was lethargic and did not open its mouth or attempt to fly until it had been warmed in hand for five minutes. The female was capable of immediate flight. On April 21 two adult female Seminole bats were found in the same moss clump but one foot apart. The air temperature was 70°, the relative humidity 43 per cent. One bat immediately flew, and the other was incapable of flight for two minutes. A few minutes earlier another Seminole bat 200 ft. distant escaped capture by flight. That low temperatures inhibit natural flight is indicated by day and night observations of undisturbed bats. A Seminole bat failed to fly the night of March 22 when the air temperature at dusk was 66°, and the relative humidity was 34 per cent. By 5:15 the following evening the air temperature had risen to 72° and the relative humidity to 53 per cent. At 11:30 PM the bat was gone and was not seen again. Another Seminole bat in moss failed to fly on a night when the air temperature at 7:05 PM was 50° and relative humidity 86 per cent, becoming progressively cooler later. A third undisturbed *L. seminolus* was found in a moss clump the morning of February 20. The air temperature the previous night had dropped to 32°. On Feb. 20 the temperature rose to 65° in late afternoon and dropped to 30° that night, but the bat did not fly. The following evening the temperature had risen to 70°, and the bat flew.

George Gorman, of the Newton Field Station, collected many bats by shooting in nearby areas during the winter of 1954–55. He noted that bats, including *Lasiurus*, were seldom seen flying at temperatures below 70°. The lowest temperature at which the writer observed what appeared to be the smaller *Lasiurus* in flight was 68°, when the relative humidity was 38 per cent.

The only *Dasypterus floridanus* observed was in the interior of a moss clump on the west side of a live oak at an elevation of 15 ft. When the moss was parted for close inspection, the bat squeaked noisely, launched downward with spread wings three feet before starting to fly, after which it flew with ease about the area, eventually disappearing behind heavy growth. At this time the air temperature was 83°, the relative humidity 54 per cent.

The single *Lasiurus borealis* discovered was an adult female, found April 11 in the interior of a moss clump on the west side of a tree at an elevation of nine feet. The air temperature was 56°, the relative humidity 78 per cent. This bat was dormant, remaining motionless after being warmed in hand for five minutes.

Captured bats.—In addition to the *L. borealis*, already mentioned, the following *L. seminolus* were taken in hand, closely examined and banded: Feb. 8, male, judged to be a young bat of the previous year; Feb. 12, adult male; March 26, one adult male, one adult female; March 30, adult male; April 1, adult female; April 11, adult male; April 19, one adult female, one immature male; April 20, aged female; April 21, two adult females.

Except for the adult male collected March 30, all *L. seminolus* taken from February 8 through April 11 were tentatively considered to be in relatively unfaded characteristic pelage. Coats of the remaining Seminole bats appeared faded in varying degrees. None appeared to be molting.

Hair obscured viewing the positions of testes in three male Seminole bats, but three others were inspected and measured, providing the following data: Feb. 8, descended to position lateral to base of tail, combined size of testicle and epididymis 1.5 × 4 mm.; Feb. 12, similar position, 2 × 4 mm.; April 19, similar position, 1.5 × 2 mm. There was no external evidence of mammary development in females, and nipples of *L. seminolus* measured 1 mm. in length, varying in width from 0.2 to 0.3 mm.

None of the bats showed evidence of disease or obvious external parasitism, although three bats had previous injuries. An adult male Seminole bat, collected March 30, had one hole in the interfemoral membrane and 13 holes in the wing membranes, appearing to have been riddled by shot. The adult female *L. borealis* had a ¼-inch hole in the right wing membrane and a hematoma on the right forearm. The young male *L. seminolus,* captured April 19, showed the following pathology: fifth digit of right manus stripped of membrane at the distal end of the metacarpal. The bare, dry phalanges had immovable joints and were dark green in color. The third tail vertebra was enlarged, forming a hard white nodule, 3 mm. in diameter. This bat flew with remarkable ease.

Bats, when active and being handled, made defensive attempts to bite, but no unprovoked attempts to bite were noted.

Captive bats.—The Seminole bat captured Feb. 8 was kept indoors for experiments. This individual preferred to hang pendant at the interstices of the fiberboard block ceiling. He was difficult to dislodge when hanging and paid little attention to disturbances of any kind. The bat showed greatest interest in flying at dusk, when he adeptly flew about the interior of the building. He occasionally reduced elevation and speed, and with lowered head and open mouth, dragged his chin along the shiny linoleum floor, apparently mistaking the shining surface for water. The bat readily drank from a dish and ate boiled egg, cooked liver and crickets.

The *L. borealis,* when well warmed, was released in a room and flew with no apparent difficulty. But on seven occasions she flew directly into a wall with an audible thud and fell to the floor with outstretched wings, occasionally with continued fluttering as she fell.

Exposure to predation.—Many vertebrates, including jays, mockingbirds, cardinals and other birds, squirrels, and a cat were seen near resting bats, but no attempted predation was observed. In most instances bats were in situations seemingly impregnable to intrusion except by man, other bats and birds. However, in two instances Seminole bats were in less secure quarters. On April 21 a Seminole bat was hanging in a shredded moss clump, which was resting against a limb, and the bat was within easy reach of any bird or climbing ani-

mal. On Feb. 22 a bat was found 3½ feet above the ground in the periphery of a moss clump, where it might have been easily available to terrestrial predators. Out of curiosity, a pet grey fox, *Urocyon cinereoargenteus*, was led beneath the clump and kept there 15 minutes, during which time it showed no interest in the moss or bat. It remained unimpressed when held for two minutes with its nose 3 inches from the bat.

Possible significance in wildlife rabies problem.—Readers are probably aware that rabid bats of many species have been found throughout the United States and other areas. Rabid Seminole bats and red bats have been taken in Georgia and adjacent states, and rabid yellow bats have been taken in Florida. Consideration is being given to the query regarding the questionable role of bats as reservoirs of the disease and agents in transmitting it to other species. A plausible explanation of the circumstances of transmission might be a defensive bat bite when a bat is attacked by a predator. The foregoing data demonstrate that *L. seminolus* is occasionally exposed to potential predation, particularly during cold weather, when the bat may be lethargic or torpid. It should be noted that the wildlife rabies season in the Southeast is during the cold months. This correlation may be coincidental and was not totally unexpected. It does not provide a final answer to the rabies question.

SUMMARY

Lasiurus seminolus, L. borealis and *Dasypterus floridanus* were found in clumps of moss in oak trees in southwest Georgia during February, March and April, but not in May and June. Bats selected sites usually on the west or southwest exposures of trees, over ground providing little sunlight reflection. Bats were apparently strictly solitary until the latter half of April. Bats showed an apparent preference for certain clumps of moss. *L. seminolus* generally does not fly when the immediate environmental temperature drops below 70°F., and this species and *L. borealis* become torpid at lower temperatures. Captured bats are described, providing data on color, reproductive organs, disease, pathology, and behavior. Certain Seminole bats selected sites where predation might easily have occurred. The occurrence of torpidity during cold weather, presumably enhancing the hazard of predation, correlates with the seasonal incidence of wildlife rabies in the southeastern United States.

U.S. Public Health Service, Carlsbad, New Mexico. Received December 17, 1956.

DENNING OF THE SWIFT FOX IN NORTHERN TEXAS

By William L. Cutter

Little information has been published about the life history and behavior of the swift fox, *Vulpes velox*. This lack of information can be attributed, in part, to the fact that for many years there have been few swift foxes to observe. Swift foxes were nearly extirpated from a large portion of their range at one time. Some workers, including myself, are of the opinion that this depopulation was brought about by coyote control measures. Robinson (1953), on the contrary,

states that populations of small predators are increased because of coyote control measures. Be that as it may, the observations herein reported are on the denning and associated behavior of the swift fox. These observations were made principally in Hansford County, Texas, at various times from December, 1953 to September, 1956.

Approximately 25 occupied dens were observed. These dens were all in open, sparsely vegetated habitats, on sloping plains, hill tops, or other well-drained situations. Grater (1939), however, reported seeing a pair of kit foxes, *Vulpes macrotis*, move their whelps to a new den because the old den was flooded by high water. A mound of earth, from 2 to 12 inches high, typically extended from 2 to 4 feet from each entrance. There were one or two open entrances for each den in the spring and some dens, probably more than one year old, had also as many as four plugged entrances. The entrances were circular or slightly ovoid and were from 7 to 9 inches in diameter. The area around dens containing whelps was littered with scats and remains of animals apparently used as food, especially rabbits and small birds. Dens were found in three general situations: overgrazed pastures, plowed fields, and fence rows with wind-formed soil banks from 1 to 2 feet high. These three situations will be discussed separately.

Overgrazed pastures—Approximately 19 dens were found in overgrazed pastures. Egoscue (1956) mentions that shadscale or other small bushes were usually within easy reach of kit fox dens in Utah. In Texas, swift foxes seemingly chose the most barren areas, devoid of any bushes or tall plants, to construct dens. Swift foxes probably spend most of the day in dens, although I have observed whelps and adults outside their dens in the daytime, but always near an entrance. When I found one den in a 160-acre pasture, search ordinarily revealed two to five additional dens. To this extent, the dens were concentrated. Three were as close as 100 yards to human habitation, and six others were no farther from windmills probably visited weekly by people. The foxes probably construct the den themselves. Warren (1942: 89) and some other observers suggest that foxes merely enlarge holes previously made by rodents or badgers. In the area concerned, however, there are few holes of rodents. Badgers dig elsewhere—where populations of rodents are high. Other animals may utilize holes dug by foxes. I have trapped striped skunks, *Mephitis mephitis*, and have observed burrowing owls, *Speotyto cunicularia*, at the entrances of abandoned fox dens.

Plowed fields.—Dens in plowed fields usually can be seen for some distance because the color of the mound contrasts with that of the darker topsoil. Only two occupied dens were found in plowed fields although several unoccupied dens were seen there. One of these dens, found on July 21, had one entrance and contained two adults and six one-third grown whelps. This family group was usually outside the den in the evening. Whenever I approached the den, the two adults disappeared into it. Some of the shier whelps also disappeared into the den but immediately peered out at me and soon came out, seeming to

forget my presence. I usually sat some 30 feet from the den and the more inquisitive whelps approached me within 15 feet. The whelps usually stayed within 15 feet of the entrance of the den. The whelps were active constantly, engaging in sham fighting, catching and eating grasshoppers, and digging in the loose soil. Larry Lowery, who plowed near this den for several days, related that the whelps did not seem to mind his presence or the sound made by the tractor. Lowery said that once, as he was plowing over the den entrance, the whelps disappeared into the den but reappeared after the plow had rolled over the entrance.

Fence rows.—Fox and badger diggings were common along north–south fence rows. Rodents are believed to have been just as numerous along the east–west fence rows and no explanation can be given for the preference of these carnivores for north–south fence rows. Only four dens occupied by foxes were found along fence rows. Two adult foxes were trapped at the entrance of one of these dens in a four-day interval. Two days after the last fox was caught, a badger was trapped at the same entrance. None of the four dens along fence rows is believed to have contained young.

Several dens with one entrance in the spring had two to four entrances by August. The family groups remained together until autumn (and possibly later) and the growing whelps, in need of more room, may have dug the additional entrances. Egoscue (1956) also found that families of *Vulpes macrotis* remained together until mid-September. One den with seven entrances was "trapped out" in the middle of July. Five nearly grown whelps (average weight, 4 lb.), one adult vixen, and two adult males were caught. The whelps of other canids usually remain in the same den for a shorter time. For example, whelps of red foxes, *Vulpes fulva,* may be moved to as many as four different dens in less than two months (Scott and Klimstra, 1955: 13–14). Whelps of coyotes, *Canis latrans,* forage with the parents when 8 to 10 weeks old (Young and Jackson, 1951: 86) and whelps of gray wolves, *Canis lupus,* leave their den when two and one-half to three months old (Young and Goldman, 1944: 103).

Philip Ogilvie and I excavated a den on October 27, 1956, on the west side of a hill in a barren, overgrazed pasture, 10 miles south and 4 miles west of Gruver, Hansford County, Texas. This den had one circular entrance 8 inches in diameter, and a total of 12 feet 5 inches of open, underground tunnels (Fig. 1). The chamber was 12 inches wide and 9 inches high; its roof was 32 inches beneath the surface of the ground. Rabbit fur and bones and fox scats were at the mouth of this chamber. The entrance to each of the plugged tunnels was collapsed. The soil was dry, compact clay loam to a depth of approximately 27 inches. Below this depth, the soil contained small stones. In contrast with a den of *Vulpes macrotis* described by Egoscue (1956) the den of *Vulpes velox* had a small mound of soil at the entrance, no shade, only one entrance, and only about one-third as much underground tunneling. The floors of the tunnel had only a slight litter of animal remains and scats, and the den was in a relatively flat, open situation. Seton (1909: 702) mentioned the den of a swift fox found at

Pawnee Creek, Colorado, which contained five whelps and had 9 feet of tunneling leading to a chamber lined with grass, 5 feet below ground.

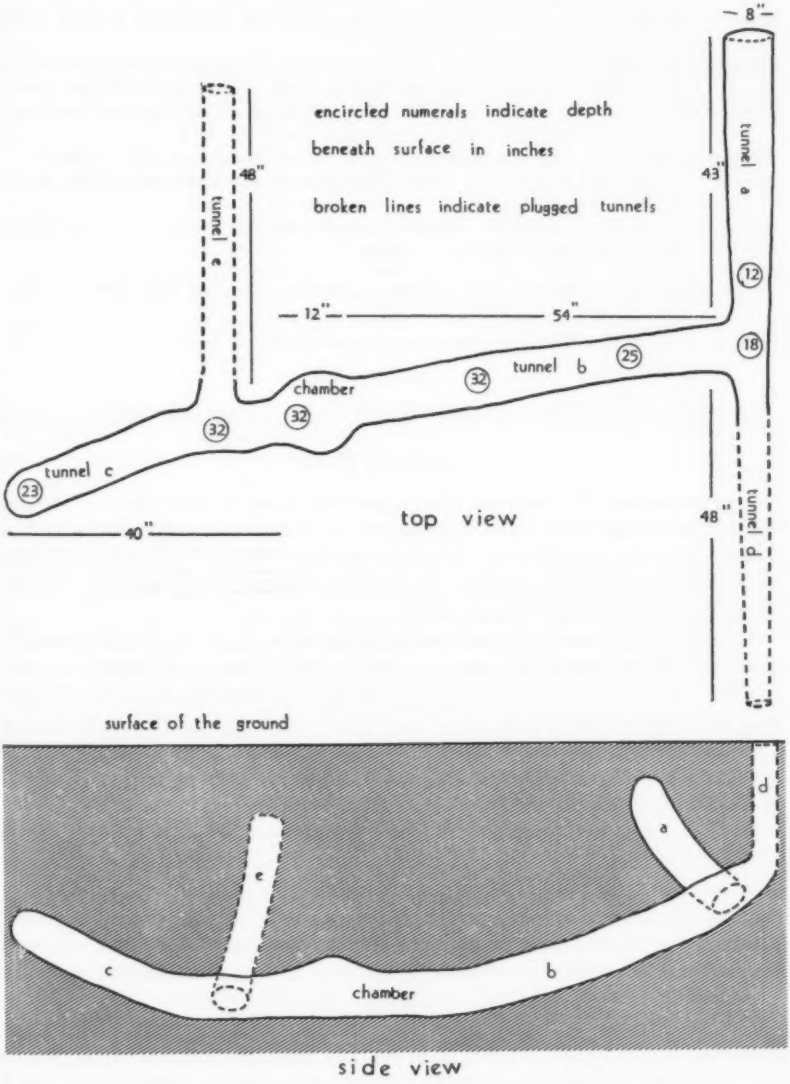

FIG. 1.—Diagrammatic drawings of a swift fox den.

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AGE STRUCTURE AND PRODUCTIVITY OF A GRAY FOX POPULATION

By John E. Wood

A knowledge of the structure of a population is essential for the clarification of population characteristics. This paper presents some of the facts learned about aging, age structure, reproduction and mortality in a population of gray fox (*Urocyon cinereoargenteus*) in southern Georgia and northern Florida between June, 1952, and March, 1956.

The base study area referred to throughout this paper as the Thomasville, Georgia, area embraces the southern portions of Thomas and Grady counties in Georgia and the northern portions of Leon and Jefferson counties, Florida. It is bordered on the southeast by Lake Miccosukee and on the southwest by Lake Iamonia. It lies in the Tift upland region of the lower coastal plains, and is characterized by a sandy soil and a typical savannah–longleaf pine disclimax of the Gulf coastal plains.

Much of the total land mass is in large plantations that have extensive stands of natural longleaf pine. Some of the plantations are managed as an economic unit and have a considerable amount of agriculture in addition to the timber production. Others, however, are managed primarily as private hunting reservations notwithstanding the potential timber revenues. On both types of plantations the woodlands are burned annually or biennially according to the management recommendations outlined by Stoddard (1931).

The study area is bisected by the Ochlochnee River and dissected by numerous small streams. Water, however, has been less abundant than normal as a result of the extended drought that has prevailed in much of the South during the period of this study.

The gray fox is the only wild member of the family Canidae to be found in this area and the population is continuous throughout; however, as is to be expected due to varying land use practices or other factors, the density of foxes is not homogeneous throughout.

ACKNOWLEDGMENTS

The present study is part of an ecological study of foxes and their role in wildlife rabies conducted by the Division of Vertebrate Ecology of The Johns Hopkins University and supported by grant E260 from the National Institute of Health of the U.S. Public Health Service.

The Communicable Disease Center of the U.S. Public Health Service has contributed its support and supplied counsel and equipment essential to the study. The cooperation of the U.S. Fish and Wildlife Service and the State Game Commissions and Public Health Departments of both Georgia and Florida have been invaluable.

Special mention is due Dr. Eugene P. Odum who made all arrangements for permission and supplied valuable assistance for the work done on the Atomic Energy Commission's Savannah River Plant; Dr. David E. Davis whose impressions are felt throughout this paper as a result of his close association with the study; and Dr. Rexford D. Lord who assisted in the field work and offered many constructive suggestions throughout the study.

CRITERIA FOR AGING

Since much can be learned of a population if its members can be aged, special emphasis was placed on the investigation of age characteristics. Previous workers (Petrides, 1950; Richards and Hine, 1953); and Sullivan and Haugen, 1956) have grouped gray foxes into juveniles or adults by examination of the teat, baculum, uterus and epiphysis. Since these characters are useful only to distinguish very young individuals, new characters were investigated. It was found that the amount of tooth attrition reflects accummulative age more than any other character examined.

In the present study 375 gray foxes collected in the area of Thomasville, Georgia, during all months of the year serve as a basis for aging. The skulls were cleaned, labeled and arranged in month groups according to the date of collection. The characters of tooth wear and skull sutures were checked and compared with such other possible aging characters as baculum weight, body weight, teat size and reproductive performance. In addition, 22 known-age animals, each one year old or older, were used as checks on these characters.

Skull sutures as age characters.—Since bone closure is generally regarded as a salient character that procedes at a somewhat constant rate, skull sutures were examined. In this study it was found that most of the skull sutures had fused by January. It was noted, however, that the suture between the basisphenoid and presphenoid lagged behind the others. To examine the suture from above and below, part of the parietal bone was removed to expose the floor of the cranium. In the late stages of closure was more readily distinguished on its dorsal surface. Apparently the sutures become closed in many cases during the tenth or eleventh month of age since 53 per cent of the one-year-old foxes possessed skulls with closed sutures; but by holding the skull to a bright light the nearly closed or recently closed sutures could be detected by the dark line of the union. The 0- to 12-month-old animals were determined by using this method and such other criteria as ovarian development, teat size, baculum weight, and tooth wear—all of which were within the limits of a 12-months animal. Collections from April and May revealed no skulls with open sutures. The opening was again recorded in June and thence onward but from obviously juvenile animals. Since all juvenile skulls collected from June through March possessed open or distinguishable sutures and none showed this juvenile quality from April until young appeared in June, those with open or recently closed sutures are regarded as animals 0 to 12 months old.

Vomer development as age character.—One skull bone was useful in distinguishing ages greater than 12 months. The vomer is a thin, plate-like bone with a medial ridge and lateral wings. At the posterior region this bone, when completely developed, is continuous with the presphenoid. During development the lateral wings extend to the presphenoid but taper medially and anteriorly toward the central ridge leaving a V-shaped gap between the anterior margin of the presphenoid and the medial ridge of the vomer.

This open condition can be found in specimens taken throughout the year. When all skulls judged by skull sutures to be 0 to 12 months old are excluded, 65 per cent of the remaining 106 skulls showed incomplete vomer development. Since not less than 50 per cent of any month's collection shows the immature vomer, it appears that this bone is not complete, at least in some animals, until at least the twenty-fourth month; otherwise in a species with a single annual breeding season there would be some month's collection in which all of the skulls would be completely developed.

Two known-age, two-year-old females examined in March revealed vomer development in its late stages which is in accordance with the expected.

Tooth wear in skulls with incomplete vomers is only slight (0 or 1, see discussion below). Thirteen skulls with complete vomer development also showed this stage of tooth wear (Table 1). If these skulls are classed in the 13- to 24-month age group according to tooth wear and collection date it indicates that 33.3 per cent of the animals completed the vomer development before they were two years old and all were complete beyond this age.

TABLE 1.—*Number and percentage of gray foxes in each age group based on skull development and tooth wear*

	FOXES	PER CENT	FOXES	PER CENT		FOXES	PER CENT IN AGE CLASSES				
Skull sutures	Open		Closed			Closed					
Vomer	Incomplete		Incomplete			Complete					
Tooth wear	0		0	1		0	1	2	3	4	
Jan.-March	16	100.0	29	58.6	42.4†	9	—	22.2	55.5	22.2	
April-June	8*	100.0	16	56.2	43.7	6	—	50.0	50.0		
July-Sept.	55	100.0	14	14.6	85.7	7	14.2	28.6	28.6	14.2	14.2
Oct.-Dec.	90	100.0	22	4.5	95.5	17	5.8	23.5	47.0	11.7	11.7
Age in months	0–12		10–24			13 and more					

* Deciduous dentition.
† 22–24 months old.

Tooth wear as age character.—The characters described above are useful age criteria but require the destruction of the animal and the cleaning of skulls. They have also the disadvantage of being limited to aging one- or two-year-old animals. The characters, however, have been valuable in establishing the age of skulls so that tooth attrition could be evaluated.

In this study the first juveniles with complete dentition were taken in mid-August suggesting that it takes 5 to 5.5 months for a gray fox to acquire its permanent dentition. Beyond this age, wear on the teeth steadily increases. The amount of wear was checked on incisors, canines, carnassials and crushing molars but only the latter showed promise for an age criterion. The character selected was the degree of wear on the protoconule and metaconule of the first upper molar. These rather large conules are protected from chipping by the greater height of the bordering major cusps. In chewing, the lateral paracone and metacone and the lingual protocone of the first upper molar straddle the heel of the lower carnassial but the conules occlude with the heel and allow regular attraction.

Several distinct stages of tooth wear were observed in each sample and collections were taken regularly for 46 consecutive months. The principal reason for the distinct stages of

tooth wear in each month's collection is the singular and rather short season of parturition (February, March and April) with a definite peak in March (see discussion on reproduction). Hence the age groups, at any moment, in a population are distinct and separated by one year. For example, in October a fox is either 7, 19, 31, 43 or 55 months old. This natural age spacing within the population allows time for each successively older group to acquire greater tooth attrition. By knowing the month of collection, one has merely to check the stage of tooth wear to determine the age in months (Table 2).

TABLE 2.—*Tooth wear applied to aging gray foxes in the area of Thomasville, Georgia*

Tooth wear	0			1			2			3			4		
	AGE	FOXES	%	AGE	FOXES	%	AGE	FOXES	%	AGE	FOXES	%	AGE	FOXES	%
June	3	8	80	15	7	88	27	3	100	39			51		
	15	2	20	27	1	13									
July	4	15	83	16	8	89	28	2	100	40			52		
	16	3	17	28	1	11									
August	5	23	96	17	3	100	29	1	100	41	1	100	53	1	100
	17	1	4	29											
Sept.	6	17	100	18	2	100	30			42			54		
	18			30											
Oct.	7	68	99	19	12	86	31	1	100	43	1	100	55	2	100
	19	1	1	31	2	14									
Nov.	8	32	97	20	4	100	32	4	100	44	1	100	56		
	20	1	3	32											
Dec.	9	4	67	21	10	100	33	4	100	45	1	100	57	1	100
	21	2	33	33											
Jan.	10	14	100	22	12	100	34	2	100	46	1	100	58	1	100
	22			34											
Feb.	11	27	100	23	15	100	35	7	100	47			59		
	23			35											
March	12	21	100	24	9	100	36	2	100	48			60		
	24			36											
April	13	3	100	25	2	100	37			49			61		
	25			37											
May	14	5	100	26	3	100	38	2	100	50			62		
	26			38											

For convenience and standardization, each stage of wear was assigned a numerical value (Fig. 1). Number 0 indicates sharp conules with no wear. Number 1 indicates conules possessing a small pit at the apex; the pit appears as though made by a pin prick. Number 2 includes conules where attrition had caused elongated areas of wear on the conule, the wear pattern being an area of exposed dentine from the apex of the conule toward the lateral cusps but with the conule still possessing its definite structure. Number 3 includes molars where a narrow band of exposed dentine joins the two conules. This stage is intermediate between No. 2 and No. 4. Number 4 includes teeth where the dentine shows as a continuous broad band between the conules, the conule itself being worn down to at least the depth of the inter-conule space (this is not the lowest spot on the tooth). In this group the dentine shows as a broad arch extending from the anterior labial to the posterior labial cusp; the deepest part of the tooth may or may not show wear.

Since several or all of these five distinct groups are represented in samples from the same area during every month and since all young are added to the population during a three-

month's period and the tooth wear of skulls ageable through two years (Table 1) fall in the first two groups, it seems reasonable to attribute the increasing degree of wear to age.

To check further into the rate of attrition (Table 1) the skulls were arranged as nearly as possible according to age using such recognized age characters as extent of suture closure, teat size and stage of development of reproductive tracts. This procedure allowed the juveniles (up to 12 months) to be grouped together. The adult skulls with incomplete vomer development were grouped as animals more than 12 and not over 24 months. This probably did not include all the animals of this age group for, as discussed earlier, some animals apparently complete vomer development before others. All older skulls (those

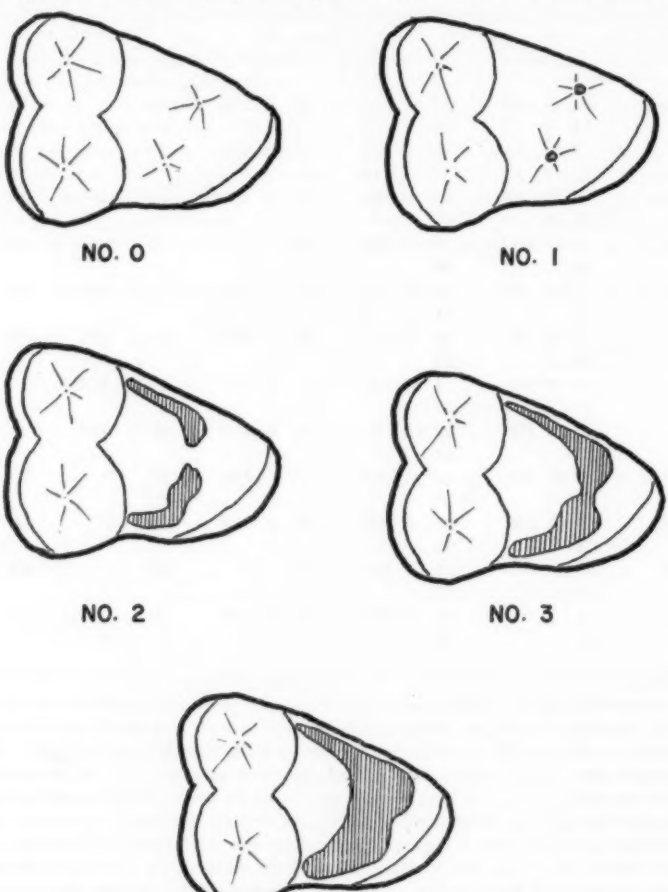

FIG. 1.—Diagram of the first upper molar of a gray fox showing the degrees of tooth wear. Shaded areas indicate the exposed dentine. The top of the figure is the front of the tooth.

completely developed) were divided into groups according to tooth wear values discussed earlier, and only in this group were the tooth wear numbers of 2 to 4 recorded. As pointed out earlier, 13 mature skulls had tooth wear of No. 0 or No. 1. In light of the tooth wear found in the first two colums of Table 1, it seems reasonable to believe that these animals had completed their vomer development earlier and thus belong to the 13- to 24- months group. Taking this assumption as a workable one and assigning skulls with tooth wear No. 2, 3 and 4 to separate age groups, Table 2 has been constructed from all undamaged skulls collected and shows age versus tooth wear.

The validity of the tooth-wear technique was checked against 22 known-age animals one year old or older and numerous animals known to be juveniles. Twelve of the check animals were recaptured wild foxes; the remaining 10 were pen-raised. Each fox was subjected to two tooth examinations with a known time interval intervening thus giving a tooth reading for two ages per fox. The mean time interval between the tooth readings was 13.5 months. These included seven foxes with a time lapse between readings of 8 to 10 months, eight foxes with a time lapse of 12 to 14 months, five with a lapse of 16 to 19 months, and one with a lapse of 33 months. At the last tooth reading the ages were as follows: five foxes, 13 to 15 months; four, 16 to 19 months; five, 23 to 27 months; five, 31 to 35 months; and three, 37 to 41 months. No difference was noted in the amount of tooth wear in pen-raised and wild foxes. For the 44 readings, only two did not conform to the expected, the difference being less than the normal wear. These data show that of the 44 ages recorded for these foxes, 93.2 per cent conform precisely in the degree of tooth wear to that of the skulls depicted in Table 2.

Baculum as an age character.—Forty-six bacula from aged animals were examined as a possible character for aging. Petrides (1950) stated that this bone can be used to separate juveniles from adult gray foxes. He gives the maximum weight of the juvenile bone as 300 mg. and the minimum weight of the bone in adults as 420 mg. The present study finds no such clear-cut distinction in weight between the two groups. Twelve animals 10 months old or less possessed bacula which weighed 0.4 grams. Seventy-six per cent of the 13 animals with bacula weights of 0.5 grams were 5 to 11 months old and 24 per cent were 16 to 19 months old. Thirteen bacula weighed 0.6 grams; 15.4 per cent were from animals 7 to 9 months old and 84.5 per cent from those 15 to 33 months old. All of the 12 bacula weighing 0.7 grams were from animals 12 months old or older. These data show animals with a baculum of 0.4 grams to be juveniles, and those with 0.7 grams to be adults. Thirty males, over one-half of the sample, with bacula weights of 0.5 and 0.6 grams, ranged in age from 5 to 33 months. However, one might assign 0.5-gram bacula to juveniles and be approximately 75 per cent correct; the error decreases, of course, as smaller bones are added to the juvenile total.

Weight as an age character.—Two litters of young born in captivity give information on the weight and age of suckling foxes. The three young of one litter did not survive and only birth weights were recorded. The other litter of five survived and their average weights were as follows: at birth, 3 oz.; 11 days, 4.5 oz.; 19 days, 5.9 oz.; 23 days, 8.2 oz.; 30 days, 8.7 oz.; 51 days, 1 lb. 4.6 oz.; and 78 days, 2 lb. 8.6 oz. The largest of these corresponds to the smallest young fox trapped which suggests that young foxes are about three months old when they first leave the den to accompany the mother on her wanderings.

Weight, with some reservations, can be used to separate age groups in juveniles and juveniles from adults. The adult weights of 93 males and 78 females and the juvenile weights of 104 males and 97 females were recorded. Each group has considerable variation as shown by the mean and standard deviation (Table 3). These weights suggest that there is little probability of capturing an adult male weighing less than 8 lb. or an adult female weighing less than 7.5 lb. It should be noted, however, that these weights are attained by juveniles five to six months after birth; consequently, weight is of little value in determining age.

AGE COMPOSITION

For information on the age structure of a fox population, a sample of 435 foxes taken in the Thomasville area was available.

Table 4 shows the percentage in each age group for the years 1952 to 1956. These data show a slight variation in age structure among years, which may be attributed to sampling error or slight fluctuations in natality and mortality. The 1952 and 1956 data are restricted because of small numbers in the former and incomplete year in the latter. For the years 1953 to 1955 there appears to have been a gradual increase in the number of juveniles and a corresponding decrease in the number of one-year-olds, but when the five years' data are viewed together the fluctuation in age classes is less prominant. When these data are grouped into one sample the results vary little from the annual percentages and show the age structure to be 61.1 per cent less than one year old; 28.3 per cent, one year old; 7.1 per cent, two years old; 1.8 per cent, three years old; and 1.6 per cent, four or more years old.

TABLE 3.—*Mean weights of gray foxes of different age groups in the area of Thomasville, Georgia*

MONTH	ADULT MALES			ADULT FEMALES		
	Foxes	Mean	St. Dev.	Foxes	Mean	St. Dev.
June	11	9.0	.78	6	8.9	.88
July	6	8.5	1.49	4	8.2	.37
Aug.	4	8.4	.24	5	9.0	1.08
Sept.	2	9.4	1.60	2	9.4	2.33
Oct.	15	9.2	1.10	11	8.2	.69
Nov.	12	9.7	1.06	7	8.8	.76
Dec.	9	9.2	1.94	6	8.1	1.20
Jan.	11	8.9	1.17	15	8.5	.65
Feb.	10	9.1	.80	11	8.7	.98
March	7	8.4	.76	7	8.2	.94
April	2	9.4	.53	2	8.8	.35
May	4	9.4	.65	2	8.3	.35
Total	93	9.1	1.10	78	8.5	.93

AGE, MONTHS	JUVENILE MALES			JUVENILE FEMALES		
	Foxes	Mean	St. Dev.	Foxes	Mean	St. Dev.
3	4	3.5	.46	4	3.3	.79
4	6	4.3	.79	7	4.7	.81
5	15	5.5	1.34	7	5.1	1.30
6	8	7.8	1.04	8	7.3	.61
7	20	8.5	.56	21	7.8	.78
8	9	8.8	.95	14	7.9	.95
9	10	8.1	1.41	10	7.5	.58
10	10	8.6	.77	7	8.1	.66
11	17	8.7	.93	8	9.0	1.16
12	5	9.3	.49	11	8.2	.50
Total	104			97		

TABLE 4.—*Age structure, in per cent, of the gray fox population of the Thomasville, Georgia, area during the years 1952–1956*

AGE, MONTHS	1952	1953	1954	1955	1956*	1952–1955
0–12	63.1	51.4	58.4	68.8	51.5	61.1
13–24	31.6	36.1	31.0	21.0	33.3	28.3
25–36	0	9.7	5.8	8.2	15.1	7.1
37–48	0	1.3	3.2	0.6		1.8
49+	5.2	1.3	1.6	1.2		1.6
Total foxes	19	72	187	157	66	435

* Incomplete year's data (January through March).

In order that the age structure of the Thomasville population might be more intelligently evaluated, the age composition of four other populations was checked (Table 5).

The Washington–Jackson County, Florida, area lies about 65 miles west of the Thomasville area. It is a lime-sink formation with many lakes and deep, loose, sandy soil. The cover types are those typical of the Dougherty Plains of which much of it is a part (Norris, 1951). The agriculture consists largely of tenant farming, and red foxes form part of the species composition in the north. Fifty-five gray foxes were taken during the winters of 1953 to 1955 and show an age structure varying but little from the other areas.

The Atomic Energy Commission's Savannah River Project lies about 225 miles northeast of Thomasville. It is predominantly coastal plain but borders the Piedmont Plateau region. It is unique in its land-use in that no persons now live on the area and the former farm lands have been allowed to pass through their successional stages (Odum, 1952). It has a sandy soil and lies partly in the flood plain of the Savannah River. The cover types consist of numerous old fields, many creeks, and ridges of pine or turkey oak. Red and gray fox are found throughout the area but the red fox is less abundant on the old river terraces than on the uplands. The age composition of the gray fox population is based on 113 foxes examined during the months of March, April and November of 1953 through 1955. Table 5 shows the same trend in age structure as was found in the other populations.

The Georgia counties of Colquitt and Mitchell represent a sampled population. The area checked lies in the northeastern part of Mitchell County and the adjacent areas of Colquitt County. This location is about 40 air miles north of the Thomasville area. It

TABLE 5.—*Age structure, in per cent, of five widely separated gray fox variations located in different ecological areas*

AGE, MONTHS	THOMASVILLE, GA.	SAVANNAH RIVER PROJECT	CLOQUITT–MITCHELL CO., GA.	BEN HILL–CRISP CO., GA.	WASHINGTON–JACKSON CO., FLA.
0–12	61.1	58.5	48.1	57.1	52.7
13–24	28.3	23.9	29.6	26.2	27.3
25–36	7.1	13.6	14.1	11.9	14.5
37–48	1.8	3.5	3.7	2.4	1.8
49+	1.6	0.8	4.4	2.4	3.6
Total foxes	435	113	135	42	55

differs in that red foxes comprise about 35 per cent of the total fox population. The land-use practices vary from those of the Thomasville area in that the land is divided into small farms as opposed to large plantations, which results in a greater diversity of crop lands and pastures and less extensive areas of woodlands. This area has a much greater density of people and consequently has more dogs and other domestic stock. In addition it has a larger number of active fox hunters. Table 5 shows a slightly lower juvenile component than was found in the other areas sampled.

The area including the Georgia counties of Ben Hill and Crisp is about 75 miles northeast of Thomasville. It is about equally divided into farm lands and turpentined woods and simulates a condition intermediate between the conditions found in the Thomasville area and the Colquitt–Mitchell area, but resembling the latter in the proportions of red and gray foxes.

Since the age groupings of a population reflect the survival of individuals, the age composition would, in a stationary population that has a constant birth rate, be equivalent to a survivorship curve; and since the variation in age structure among basically different ecological areas with and without red fox competition is no greater than the annual variation found in the Thomasville area (Tables 4 and 5) it seems reasonable to assume that the age distribution here expressed is a characteristic of gray fox populations, at least in the Coastal Plains region of the South.

SEX RATIO

Sex ratios were checked among different areas and different seasons to determine any differences that may be manifested. Gray foxs collected from 11 widely separated areas in Georgia, Florida and South Carolina numbered 1,818, but none of the localities or the combined total showed a proportion of males that was significantly different from 50 per cent. When the data were examined on a monthly basis there was a significant predominance of males only in February.

The data were grouped so that the cool weather and breeding season sex ratios could be examined. During the months October through February, 281 males represented 53.9 per cent of the catch, which is not significantly different from 50 per cent. The sex ratios were not significantly different from 50 per cent for the trapped animals taken during the whelping and denning period (February through May) and the summer (June through September).

The primary sex ratio was determined from 43 embryos from nine litters. Of these, 51.1 per cent were males, which is not significantly different from 50 per cent.

REPRODUCTION

Since reproduction is a basic phenomenon of a population and therefore fundamental to an ecological study, the gray fox population of the Thomasville area was examined for its reproductive performance. The reproductive organs of 126 adult females collected in all months were examined and the uterine and ovarian data recorded.

Age at sexual maturity.—The analysis of age at sexual maturity is based on an examination of 78 females 10 to 21 months old and thus in their first breeding year. They were considered sexually mature if the ovary possessed Graafian follicles, corpora hemorrhagica or corpora lutea of early pregnancy, or if the developing follicles showed definite signs of maturing, a phenomenon accompanied by a turgidity of the uterus. They were naturally recorded as mature if gravid or postpartus as indicated by the presence of placental scare. If none of these conditions was observed, they were regarded as nonbreeding females. Table 6 shows that 92.3 per cent of the females in their first breeding season produced litters or showed definite signs of maturation.

Only limited data were collected on sexual maturity in males. Sperm were present in small amounts in two of the nine young foxes collected in November. All of the five young males checked in December, January and February possessed sperm. No sperm were

found in the four yearlings taken in March, April and May, but these might have been productive earlier in the season. It is worthy to note that sperm are present when the vas deferens of the epididymis can readily be seen as a twisted tube.

Time and extent of breeding season.—The extent of the breeding season was determined by morphological indicators in the uteri and ovaries. The earliest breeding dates recorded were those of a female possessing four small embryos on January 6 and of one with six small embryos on January 8. These females probably bred during late December. The pregnancy data, however, suggest that most breeding is later with the peak occurring late in January or early in February. The earliest whelping data recorded was March 21. Allowing 53 days for gestation (Sheldon, 1949), the breeding date would have been January 27. Postpartus females trapped March 24, 25 and 27 showed recent placental detachment which indicated that parturition had occurred within the past few days. These females would have been bred during late January.

Breeding in the Thomasville population continued into the first half of March as indicated by five March specimens with corpora hemorrhagica or corpora lutea of early pregnancy and two females with Graafian follicles. In April, five of the eight females examined were gravid but no embryos were recorded later in the year.

No difference was noted in the time of breeding among 56 yearlings and 44 older females collected between the first of January and the end of April. One of the early January pregnancies was a 10-month-old animal; the other, unfortunately, was not aged.

The peak months of breeding can be determined by noting the percentage of females that are oestrum or are gravid. In January, 13 per cent of the 15 females examined were gravid; this increased to 46 per cent of the 13 examined during February and to 67 per cent of the 40 examined in March. None of the 73 females captured after March was gravid. In January, 80 per cent of the females were in oestrum. They decreased to 46 per cent in February and to 20 per cent in March. No females were observed in oestrum later than March. This suggests late January and early February as the peak period in breeding.

Productivity of a population.—One hundred fifty-one females from the Thomasville area were grouped according to age. Their reproductive performance was recorded so that a better understanding of the population's reproduction could be obtained.

Table 6 records the females of the various ages and their performances. Barren females were absent only in the two-year-old group. The entire sample, representing all ages of the population, shows that 6.4 per cent of the females failed to reproduce. Sheldon (1949) found 3.3 per cent barren females in the gray fox of New York.

The females examined gave evidence of the number of young produced per litter (Table 7). The data on numbers of embryos and placental scars were analyzed separately (Table 6) but the difference between them was not significant ($t = .11$ with 99 d.f.). The two sets of data were then combined to give a mean litter size of 4.56 with a standard deviation of 1.09. This is a larger mean litter than was recorded by either Sheldon (1949) in New York or Richards and Hine (1953) in Wisconsin. Their figures were 3.66 and 3.9, respectively. In population studies it is important to know the fecundity of the different age groups. Table 7 shows the mean number of young (embryos and placental scar counts) produced by each age. By the group comparison analysis the t values for the one- and two-year groups ($t = .99$ with 85 d.f.) and one- and three-year groups ($t = 1.47$ with 68 d.f.) were not significant at the 0.5 level which indicates no difference in the fecundity of these groups.

Resorption of embryos was recorded for three gravid females. Two females had five and one had six well-formed embryos with crown-rump measurements of 13, 19 and 26 mm. In addition, each female possessed one well-developed placenta with no recognizable embryo. The area in which the embryo would have lain was filled with a thick, dark, sticky paste. In addition to the gravid females, one postpartus female showed signs of embryo resorption. One of the four placental attachment area was not over one-half the size of the others and was covered with the same thick, dark, sticky paste. Since the placental attachment of a

TABLE 6.—*Breeding performance by age classes of the gray foxes of the Thomasville, Georgia, area*

AGE YEARS	NO. FOXES	NO. GRAVID	EMBRYOS*		TEST [illegible]	PLACENTAL SCARS*		OESTRUM	NO SIGNS OF BREEDING	% NOT BREEDING
			Mean	S.D.		Mean	S.D.			
1	78	25	4.76	1.02	36	4.19	1.18	11	6	7.69
2	39	11	5.27	1.12	19	4.44	0.89	9	0	
3	22	4	5.75	1.49	11	4.66	0.86	5	2	9.09
4	3	0			1	5.00		1	1	33.33
Total	141		4.90	1.12		4.31	1.01		9	6.35

* Group comparison of embryos and placental scars shows no significant difference. $d.f. = 99$, $t = 0.11$ (combined embryos and placental scar counts = 4.56s = 1.09).

resorbed embryo is likely to be counted as a young produced in a placental scar count, some error can be expected when placental scar counts alone are used to estimate litter size.

As pointed out earlier, the largest portion of the sexually mature population is animals in their first breeding year (less than 12 months of age) with a steady decline for successively older ages. And since only 7.69 per cent of the yearling females are nonproductive, the largest part of the population's juvenile crop should be the offspring of the one-year-old females. After correcting for sexually immature or otherwise barren females, and regarding age groups by breeding seasons closest to their true age group, it is found that 54.5 per cent of the population's young are produced by females in their first breeding season; 33.6 per cent by the two-year group; 11.2 per cent by the three-year group; and 0.7 per cent by the four-year group.

Mortality.—The probability of dying has been determined for the foxes of the Thomasville area by analysis of the age composition of the foxes in Table 4. Because foxes are difficult to trap in summer, only foxes caught from October to March inclusive were used, thereby reducing variability due to differential trapability in summer and in winter. The age-composition method of course assumes that no changes occur in reproductive or mortality rates in the various years. The available data (Tables 4 and 6) suggest that changes may

TABLE 7.—*Number of young produced by different age groups of gray foxes*

NO. OF PLACENTAL SCARS AND EMBRYOS	AGE OF FOXES, YEARS				TOTAL
	1	2	3	4	
2	2	—	—	—	2
3	9	3	—	—	12
4	20	8	7	—	35
5	16	12	4	1	33
6	5	4	1	—	10
7	4	1	1	—	6
Total	56	28	13	1	100*
Mean	4.44	4.71	5.00	5.00	4.56
Standard deviation	1.22	0.976	1.11		1.09

* Total includes 2 animals of unknown age.

be as much as 12 per cent. However, for an average mortality figure these changes can be smoothed by tabulating foxes from several years and ignoring the problem of weighting the numbers. Such calculations are admittedly crude but are satisfactory if not too much is claimed for their precision.

Data for the observed numbers of foxes and the average age of those foxes (Table 8) can be used to determine probabilities of dying. It is noted that from the first November to the second November of a fox's life the probability of dying is about 0.7. For succeeding years the figures vary but a smoothed curve gives about 0.5 for adults. No difference between males and females was apparent.

These results can be used to calculate number of foxes alive on March 1 of each year. The number born can be obtained from the number of adults alive on March 1. Since 196 young and 78 adults were present in winter (average November 1), we can assume that these 196 young are the survivors of those born March 1 and the 78 adults are the survivors of those that bred on March 1. Using $q = 0.7$ (annual) we can calculate that 173 adults were alive on March 1 (eight months before). Assuming that half were females and that 96 per cent of them produced 4.5 young, we calculate that this population produced 375 pups. These were reduced to 196, 8.2 months later. On this assumption, the probability of dying, for pups for the first 8.2 months, is at an annual rate of 0.63.

However, there is reason to believe that the mortality of adults in summer is lower than in winter. If we assume that from March to November mortality of adults occurs at an annual rate of only 0.5 then 128 adults were alive on March 1 and produced $(128/2)(.96)(4.5) = 277$ pups on March 1. These were reduced to 196, 8.2 months later. On this assumption, the probability of dying, for pups for the first 8.2 months, is at an annual rate of about 0.40.

The mortality of pups during their first winter needs to be considered. If we have a population of 173 adults on March 1, 52 of them will be survivors of the 78 adults alive on November 1 of the preceding year, using q (for adults) of 0.7 during winter. Therefore, 121 must be survivors of the 196 pups alive on November 1. Thus, during their first winter the pups had a probability of dying of 0.40 or at an annual rate of 0.77.

Using the other assumption, we have a population of 128 adults on March 1 and 52 are survivors from the 78 alive in November. Then 76 will be survivors of the 196 pups alive on November 1. Therefore, during their first winter, the pups had a probability of dying of 0.61 or at an annual rate of 0.94. In either case it appears that the winter mortality of pups is high.

The data on age composition in various places (Table 5) are consistent with the above estimates when it is remembered that most of the age 0–12 month foxes were actually caught in fall and winter. In Table 8 is given an hypothetical age composition using the

TABLE 8.—*Average age of foxes caught in winter at Thomasville, Georgia, according to year of life*

YEAR	AVERAGE AGE, MONTHS	NO. FOXES	d_x	q_x	AGE, MONTHS	CALCULATED FOXES	PER CENT IN AGE
0	8.2	196	140	.71	0	375	70
1	20.6	56	46	.82	12	117	21
2	31.5	10	5	.50	24	32	6
3	45.0	5	—	—	36	11	2
4	57.0	7	—	—	48	3	1
						539	

estimates derived above. It is not intended to push this analysis too far because the sample size is small and the basic assumptions (no change in birth or mortality rates) are not completely satisfied. It does seem permissible to conclude that the probability of dying (annual basis) of pups in their first summer is about 0.5, in their first winter about 0.9, and of adults is about 0.5.

SUMMARY

During the years 1952 to 1956 the gray foxes of the Thomasville, Georgia, area were studied to determine the structure and productivity of the population.

The foxes were aged by the amount of wear on the conules of the first upper molar. Five categories were recognized, each representing an age interval. Other aging techniques discussed involved skull sutures, development of vomer, weight of baculum and body weight, but all have limitations making them less desirable than tooth wear.

Young gray foxes had a weight at birth of 3 oz.; this increased to 2 lb. 8.6 oz. at 78 days of age. Juveniles reach adult weight at the age of five to six months.

The age structure for five separate gray fox populations of the southern coastal plains is given and each is similar to that of the Thomasville, Georgia, area where the population is represented by 61.1 per cent less than one year old; 28.3 per cent one year old; 7.1 per cent two year old; 1.8 per cent three years old; and 1.6 per cent four years old or older.

The sex ratio of 818 gray foxes collected over a wide area of Georgia and Florida shows a ratio of males to females which is not significantly different from 50:50.

Sexual maturity is reached during the first year, and only 6.3 per cent of the total number of females of all ages failed to breed.

Breeding first occurs in late December but the peak of the breeding season is late January and February. No significant difference was found among the number of embryos and number of placental scars; combined they give a mean of 4.5 young per litter. No difference was found in the fecundity among age groups; but due to the greater number of young females, 54.5 per cent of the young born are produced by one-year-old females; 33.6 per cent by two year olds; 11.2 per cent by three year olds; and 0.7 per cent by four year olds.

The probability of dying from the first November of a fox's life to the second November is about 0.7. For succeeding years it is about 0.5. The probability of dying (on an annual basis) during the first summer is about 0.5 and during the first winter about 0.9.

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A FOSSORIAL MAMMAL OF UNKNOWN AFFINITIES FROM THE MIDDLE MIOCENE FAUNA OF NEVADA

By Charles A. Reed and Theodore Downs

A reconnaissance collecting trip in the fall of 1953, by personnel of the Los Angeles County Museum at the type locality of the Stewart Spring, late Middle Miocene fauna of western Nevada, resulted in the recovery of a collection of small mammal remains. Among these remains is an incomplete left humerus of an unknown genus of fossorial mammal (L.A.C.M. No. 1380). The junior author collected the specimen and assumed at the time that it was a mole-like animal. However, further examination and comparison by the authors (Reed in particular) revealed that this likeness is indicated only in the antero-posterior flatness of the shaft of the bone. Details of the structure are unique and are not known in any genus of mammal so far described, including the equally distinctive and more ancient *Cryptoryctes* and *Arctoryctes*, and the members of the family Talpidae. However, we consider it unwise to describe a new genus on the basis of this one fragmentary humerus.

The specimen was taken at the original University of California Museum of Paleontology loc. V2027 (L.A.C.M. loc. 1104), Esmeralda County, Nevada; in the Esmeralda formation near Stewart Spring and Finger Rock Wash; Tonopah quadrangle, T. 8 N, R. 36 E. It shows evidence of polishing from some type of abrasive-wearing action, probably during deposition in water. Other mammals collected show similar effects of deposition and wear. Previous authors (e.g., Stirton, 1939) have reported the following mammals from Stewart Spring: Insectivora, ?*Meterix*; Carnivora, *Cynodesmus* cf. *kelloggi*, *Bassariscus parvus* Hall; Rodentia, *Liodontia*, *Monosaulax* cf. *pansus*, *Mylagaulus*; Perissodactyla, *Hypohippus* cf. *osborni*, *Merychippus brevidontus* Bode, *Merychippus* cf. *californicus*; Chalicotheriidae; Artiodactyla, *Merycodus nevadensus*.

DESCRIPTION AND COMPARISON

Although close study now reveals certain definitive mammalian characters of this humerus, the allocation to the Class Mammalia was not at first clearly evident. The humerus to be described (L.A.C.M. No. 1380) is missing the head, medial epicondyle, teres tubercle (the latter if it were ever present), and most of the greater tuberosity. Probably a small lateral epicondyle was originally present although defacement has made it difficult to determine this.

Three other talpid-like fossil species are important for comparison with No. 1380. *Cryptoryctes kayi* Reed (1954) from the early Oligocene of Montana is represented by several fragments of humeri; *Arctoryctes terrenus* Matthew (1907), from the early Miocene of South Dakota, is based on a left humerus; and *A. galbreathi* Reed (1956), based on four humeri, is known from the mid-Oligocene of Colorado and Montana. These two genera are burrowing forms but still distinct from the moles. *Arctoryctes* may have descended from

Cryptoryctes (Reed, 1954*a*), or the two may have diverged from a common ancestor (Reed, 1956). These genera cannot be assigned to any known mammalian order, although they probably represented the Insectivora (or, possibly, Edentata); their functional character and morphology suggest convergent evolution toward the talpids.

The entire bone under discussion in this paper is "weak" as compared with the humeri of *Cryptoryctes*, *Arctoryctes*, and specialized talpids such as *Scapanus*, *Scalopus*, or *Talpa*. The shaft is much flatter (slightly concave on the posterior surface) and the lateral edge is almost straight from the greater tuberosity to the capitulum (anatomical nomenclature follows that of Reed, 1954*a*). Such a character is regarded as unspecialized in contrast to the extremely inturned lateral boundary of *Cryptoryctes*, *Arctoryctes*, and the talpids. The Nevada specimen is definitely not as expanded distally as are the humeri of *Cryptoryctes* and *Arctoryctes*, but is somewhat wider (actually and in proportion to its length) at the narrowest place across the shaft. It is impossible to know the extent of the medial epicondyle and the teres tubercle since their extremities are absent in the Stewart Spring specimen.

If the head and greater tuberosity were complete, this specimen (No. 1380) would be a little longer than the humerus of *A. terrenus*. Measurements of No. 1380 are as follows: greatest available length, 11.9 mm.; least width across shaft, 6.0 mm.; greatest available distal width, 7.5 mm.; greatest available proximal width, 7.4 mm.

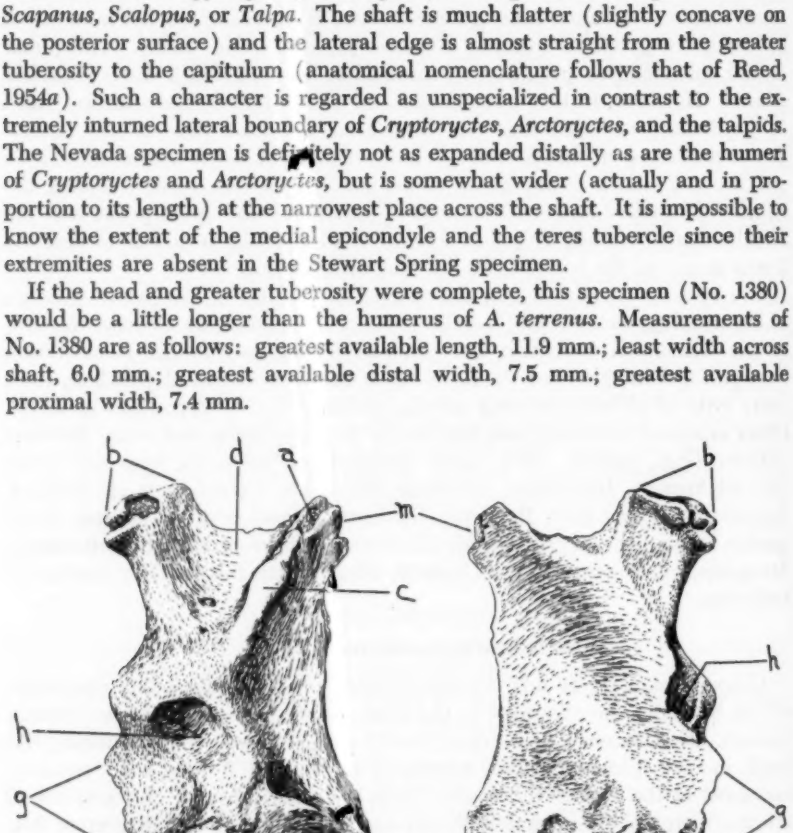

FIG. 1.—Left humerus of unknown mammal, L.A.C.M. No. 1380. Anterior aspect (left) and posterior aspect (right); *a*, base of greater tuberosity ?; *b*, lesser tuberosity; *c*, pectoral process; *d*, bicipital groove; *g*, medial epicondyle; *h*, supracondyloid (entepicondylar) foramen; *i*, trochlea; *k*, capitulum; *l*, lateral epicondyle; *m*, base for head ?; *o*, groove of unknown function. × 5.

The capitulum (Fig. 1, *k*) is an elongate ovoid bulb, quite similar to the capitula of *Cryptoryctes, Arctoryctes,* and the specialized moles, and indicates a similar type of articulation with the radius.

The lesser tuberosity also resembles in a general way the same structure in these other burrowing mammals, but in this Miocene specimen there is no approximation of the lesser tuberosity to the pectoral process to form even a suggestion of a bicipital tunnel to carry the long head of the M. biceps brachii. Since the development of a bicipital groove or tunnel, at least to some degree, is the most basic talpid character (Reed, 1954*b*), leading to the specialized evolution of the family, the Miocene humerus under consideration cannot have any relationship to the moles.

The pectoral process lacks the distal expansion so prominent in the humeri of *Cryptoryctes* and *Arctoryctes.* The undeveloped nature of this prominent process seems to indicate less powerful pectoral and deltoid muscles, inserted less distally. The lack of development of this process also has some meaning in relation to the function of the biceps brachii muscle, since the biceps has to pass medially around the distal end of the pectoral process in order to reach the point of insertion. There is no definite distal extension of the pectoral process for the tendon (or possibly part of the fleshy belly) of the biceps brachii muscle to pass around in No. 1380. This condition, in correlation with the lack of even an incipient bicipital tunnel, would indicate almost complete absence of any twisting or counter-rotatory action by the biceps in the recovery stroke (Reed, 1951: 642), as found in specialized talpids.

The trochlea is uniquely shaped, yet definitely a mammalian trochlea. It is completely different from the trochlea typical of other mammals (*Cryptoryctes, Arctoryctes,* specialized talpids) that burrow by a rotatory action of the humerus (Reed, 1951, Fig. 5; 1956, Fig. 130). The primary differences between the trochlea of No. 1380 and that of almost any other mammal are: (1) On the anterior aspect, the chief articulating surface for the semilunar notch of the ulna is a large tuberosity (Fig. 1, *i*) instead of the typical mammalian "roller-type" or pulley from which the structure derives its name; this tuberosity, however, is definitely an articular surface; (2) on the posterior surface, the trochlea is continued as a shallow groove (Fig. 1, *i*), obviously for articulation with the proximal aspect of the semilunar notch, but without the typical definite boundaries and without the semicircular articular surface that the typical trochlea has. Thus the semilunar notch of the ulna was not a part of a circle, but must have been more shallow and open.

In correlation with the peculiarities of the trochlea and the assumed open semilunar notch of the ulna, an olecranon fossa is absent. Such an anatomical peculiarity would seem to mean that the proximal lip of the semilunar notch was poorly developed, if at all, and possibly that the antebrachium could not be completely extended. All hitherto known fossorial mammals that burrow by a rotatory action of the humerus (with one possible exception) have a well-developed semilunar notch, and a very tight, strong joint between notch

and trochlea. In the present specimen the joint would seem to have been loose and weak, comparable functionally to the similar condition in a Paleocene humerus of unknown affinities from Montana (Reed, 1954 *a*) which also lacks an olecranon fossa, but otherwise the two humeri are dissimilar in detail and no phylogenetic relationship is suggested.

The Miocene humerus from Nevada lacks the disto-medial pit, for the attachment of the great ligament of the M. flexor digitorum profundus (Reed, 1951: 654–656; 1954*a*: 103), which seems to be otherwise universally present in fossorial mammals that burrow by rotating the humerus. A groove (Fig. 1, *o*) on the posterior surface, medial to and deeper than the trochlear groove, might be construed as a place of attachment for such a ligament, if present, but this groove does not correspond in position or shape to the pit in question (Reed, 1951, Fig. 5, *j*; 1954*a*, Fig. 7, *j*; 1956, Fig. 130, *j*), and the M. fl. digitorum profundus may not have had any such tendon, with its remarkable function of flexion of the digits during the burrowing stroke (Thompson, 1884). The true function of this groove (Fig. 1, *o*) must remain problematical; such a groove is unknown to us on any other mammalian humerus.

Another outstanding and distinctive feature of No. 1380 is the extremely proximal position of the supracondyloid foramen. It is even proximal to the probable teres tubercle and it seems actually to traverse the base of the tubercle. Furthermore, the foramen is nearly parallel to the long axis of the humerus in contrast to the condition in *Cryptoryctes*, *Arctoryctes*, and talpids, in which the foramen tends to be nearly horizontal. In *Cryptoryctes* and *Arctoryctes* the foramen marks the boundary between the teres tubercle and the medial epicondyle.

The brachial fossa is undeveloped although, if the greater tuberosity were complete, we might find that there was a greater area for origin of the brachialis muscle than now appears to have been present.

The head is missing, as it often is in fossil humeri, but No. 1380 is unusual in the very small area to which the head must have been attached.

It is indeed unfortunate that the medial side, particularly the area where one would expect to find the teres tubercle, is broken, for in a fossorial mammal this process is one of the most informative parts of the humerus. From its size and position one can tell much of the type of the burrowing stroke (here assumed to be rotatory, as in *Cryptoryctes*, *Arctoryctes* and the specialized moles) and of the size and strength of the muscles (teres major and latissimus dorsi) responsible for that rotating action.

SUMMARY AND CONCLUSIONS

A partial left humerus (Los Angeles County Museum No. 1380) of an unknown small mammal was found in the Esmeralda formation, Stewart Spring locality, of western Nevada. The age is late middle Miocene. The humerus is described in detail, but the animal to which it belonged is left unnamed, although undoubtedly representing a new genus and perhaps family.

In reviewing the Stewart Spring's humerus, it is evident that this peculiar fossil embodies a remarkable complex of characters unknown in other mammals. We believe that the animal was probably fossorial, and burrowed by means of rotatory strokes of the humerus, similar in principle to the burrowing mechanism of *Cryptoryctes, Arctoryctes* and the fossorial talpids, although the Stewart Springs mammal was probably less specialized. Actually, the flatness of the humerus, the shape of the capitulum, and the separation of capitulum from trochlea are the only evidences for this assumption of mole-like burrowing, as the other anatomical peculiarities of the humerus typical for this type of burrowing (*a*, development of the teres tubercle; *b*, shape and position of the head; *c*, presence of a pit for attachment of the ligament of the M. fl. digitorum profundus) were either not preserved (*a* and *b*) or were not present (*c*). But, in contrast, in all mammals that burrow by terrier-type fore-and-aft movements of the forelegs, the humeral shaft is always round and the capitulum and trochlea are more similar to those found in any small generalized therian.

No statement can be made as to any possible affinities of this strange humerus within the Class Mammalia. One's natural assumption is to attempt to link it to the Insectivora because the moles belong to that order and also burrow by rotating the humerus, and other mammals of unknown affinities (*Cryptoryctes* and *Arctoryctes* of the Oligocene and Miocene, and an unnamed specimen from the Paleocene) that presumably burrow in this fashion have been suggested to be Insectivora. Such reasoning does not prove anything, however, and actually the ordinal relationships of all of these mammals are quite unknown.

This specimen from Stewart Spring constitutes the most recent record of a number of peculiar fossorial non-talpid mammals from the Tertiary of North America. These mammals, known only by their humeri, are: an unnamed specimen from the Fort Union series of the middle Paleocene; *Cryptoryctes* of the early Oligocene; *Arctoryctes* of the middle Oligocene and early Miocene; and the presently described but unnamed specimen from the late middle Miocene of Nevada. The finding of such strange bones, representing such peculiar types of mammals, illustrates what discoveries can yet be made by the collector of vertebrate fossils.

The authors are indebted to Dr. Hildegarde Howard for criticism of the manuscript. We are particularly grateful for the ink drawings made by Mr. Dwight Philip, artist at the Los Angeles County Museum.

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MOLT PATTERNS IN THE BARROW GROUND SQUIRREL

By Bernard B. Butterworth

The Barrow ground squirrel, *Spermophilus undulatus kennicotti* Ross (= *Citellus parryi barrowensis* Merriam), is a resident of far northern Alaska in habitats where burrowing is possible during the summer months. It is active only five months of the year, first appearing above ground in early May, and rarely is seen after September 15. During this brief time the animal undergoes two molts, a spring molt in June or July and a winter molt in August or September.

Personnel from the University of Southern California, under the direction of Dr. William V. Mayer, have been actively engaged in the study of this particular animal over a period of several years. During this time the University has accumulated a large number of study skins and presently maintains a colony of living animals. In this investigation 142 pelts were examined. Eighty-four skins were from the Meade River area 40 miles south of Point Barrow. Six skins were captive animals at Point Barrow; ten were from Umiat; five were from East Oumalik 100 miles south of Point Barrow; and one was from Paxson Lake. Thirty-six skins were not considered because of the unusual nature of experimental research on these animals. The skins are located in the mammal collections of the Allan Hancock Foundation, University of Southern California.

Hansen (1954) described three basic molting patterns that occur in ground squirrels: (1) Those that show a diffuse pattern of hair replacement and molt once a year; (2) those that molt once a year but have a distinct molt line; and (3) those that have definite molt lines and replace their hair twice a year with two distinct coats, a summer and winter pelage. *Spermophilus undulatus* generally follows the pattern of Hansen's third type. Although the molt lines are distinct, they do not show smooth straight lines as in other ground squirrels. Hansen states that ground squirrels of the group with two annual molts are extremely southern in distribution and that most of the members do not hibernate even for short periods of time. The Barrow ground squirrel does not conform to Hansen's statement of distribution, since it is of extreme northern occurrence and hibernates for approximately seven months of the year.

Because there are sharp lines of demarcation between summer and winter hair, molt lines and patterns can easily be seen by gross visual examination. Study skin pattern plots were made for each individual on special data sheets and these were correlated according to various criteria such as age, sex and size increments. Molting patterns, when they occurred, were fairly consistent in all individuals. Many of the skins showed no evidence of molting.

Spring molt.—When the animal emerges from hibernation early in May it may either be beginning, or very shortly begins, to lose its winter pelage. The long silky guard hairs and thick woolly underfur are gradually shed. In many cases the short coarse hairs of the summer pelage are already growing

under the winter coat. The woolly underfur is absent under the new guard hairs.

Molting begins anteriorly (Fig. 1) with new hair appearing on the nose around the muzzle and extending in a narrow straight line posteriorly through the eye to encircle the ears (Stages 1A and 1B). On the forehead the molt line splits to form a complete circle around the eye. At first the center of the top of the head retains the old hair (Stage 1A) but gradually the new hair extends posteriorly and medially on the top of the head behind the ears (Stages 2A and 2B). New hair can also be seen on the front feet and legs. Molting occurs on the extremities in narrow bands parallel to one another. The new hair, under the old, extends posteriorly along the mid-dorsum. This new hair is not only shorter, but it may be of a completely different color than the older pelage which it replaces. In some cases loss of hair is so rapid that bare areas are exposed. In some of these bare areas new hair is just beginning to appear; in others, the skin is completely hairless. The new hair extends under the chin and posteriorly on the venter as well. Replacement on the venter occurs in sequences of parallel bands which proceed posteriad. Replacement on the venter is more rapid than on the dorsum. This was particularly true of females which were post-partum. The new hair grows posteriorly along the mid-dorsum (Fig. 2) and forms several small patches in the vicinity of the flanks (Stages 3A, 4A and 5) underlying the old winter coat. Strips of old hair remain along the sides for a considerable time before they are replaced (Stages 3B and 4B). Before new hair appears on the rump, the new hair replaces the old along the sides and on the hind legs and feet. The new hair on the rump extents caudad in a triangular pattern (Stage 6). The last hair to be replaced is on the thighs near the rump. In a few cases it appears that hair is never replaced on the rump. The winter molt begins before the spring molt is completed. The manner of hair replacement on the tail, if it occurs, was not obvious. When spring molting is completed, the pelage appears shiny and fresh. The hair is short with relatively little underfur and the coloration is bright. Apparently, in many individuals, some posterior guard hairs on both sides are never shed.

There is no evidence that field collected females molt earlier in the season than males, although the female skins examined show more characteristic molting patterns than the males.

Winter molt.—Study skins do not clearly show the pattern of hair replacement that occurs before hibernation at the end of the summer. Many animals collected in late August or early September are already in characteristic winter pelage. The short, coarse guard hairs have been shed and replaced by the thick woolly underfur and long silky guard hairs. Molt lines do not exist. Hair is replaced uniformly and evenly over the body. Apparently the replacement is rapid. The winter molt occurs in reverse of the spring molt. This indication is demonstrated by many individuals which show winter pelage posteriorly while regions about the head are still in the summer condition. This cephalad replacement of hair leaves the head as the last part of the body

to change pelage. One young female animal acquired from Alaska during the summer of 1956 shows a slight pattern on the head which may be a molt line.

Juvenile molt.—The young Barrow ground squirrel is born naked in June or July and begins to acquire hair by the second day (Mayer and Roche, 1954).

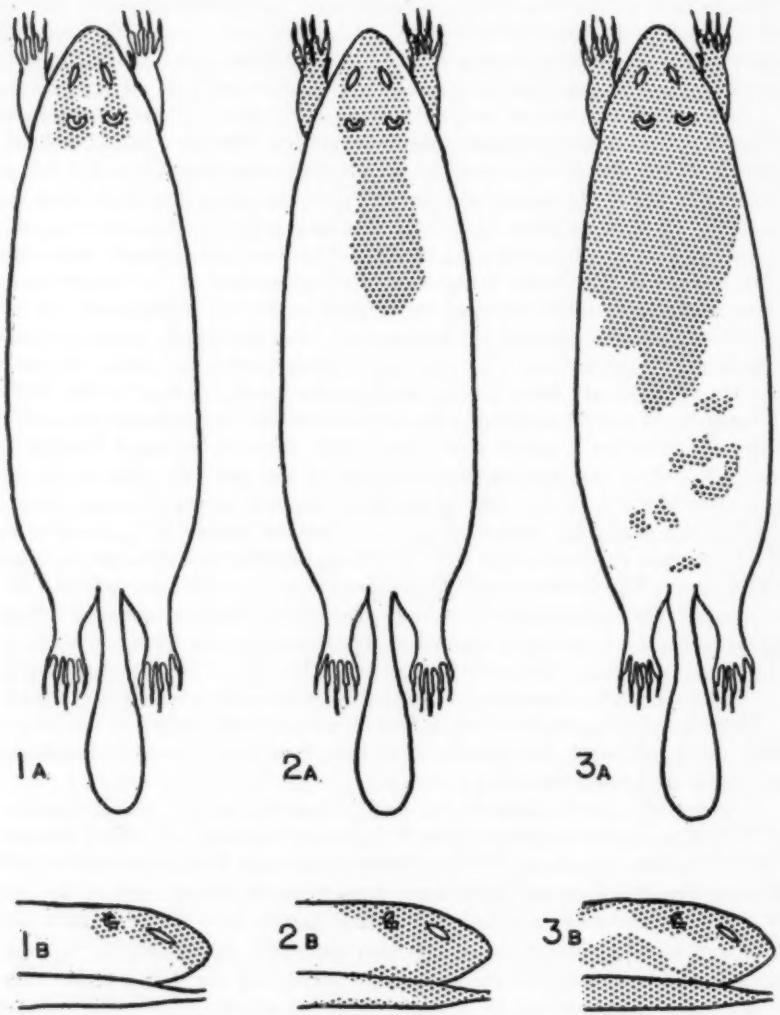

FIG. 1.—Early stages in spring molt. Stages 1A, 2A, 3A, dorsal views. Stages 1B, 2B, 3B, lateral views of head. New hair indicated by stippling.

Body growth is very rapid (Mayer, 1952). Hair growth also proceeds rapidly and by the tenth day the body is completely haired. The baby ground squirrel develops a thick undercoat which is sometimes quite dark. Spotting is very distinct and the coat has the appearance of a winter pelage due to its thickness. As the animal grows, the hair shows signs of wear and the spotting becomes

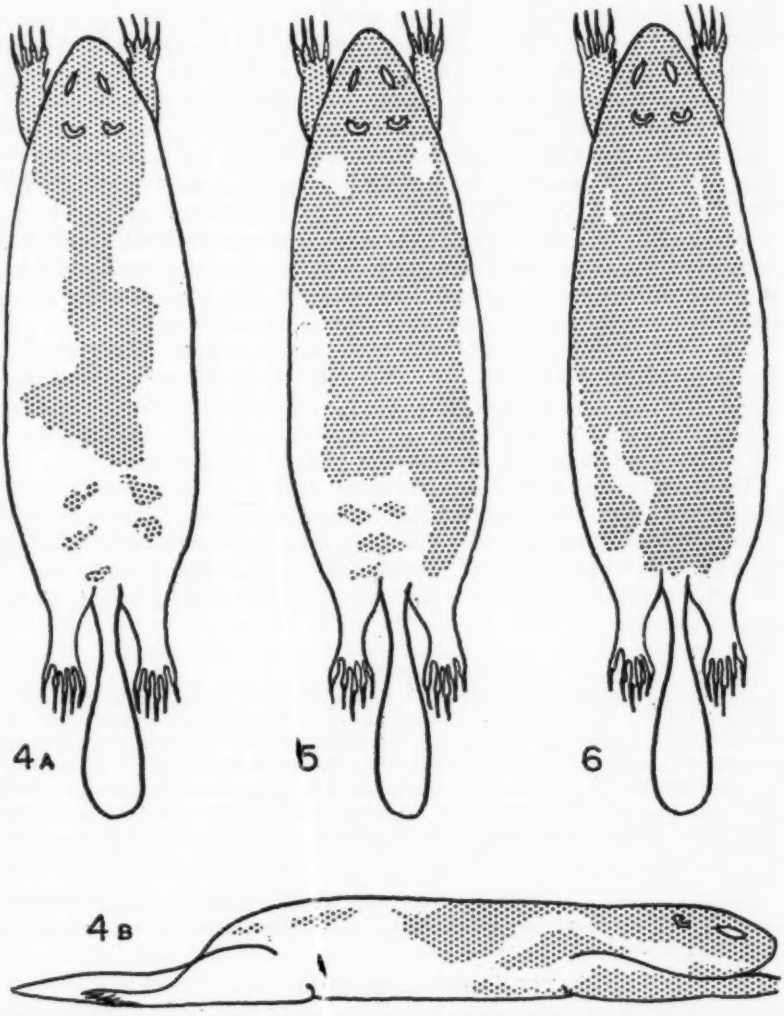

FIG. 2.—Later stages in spring molt. Stages 4A, 5, 6, dorsal views. Stage 4B, lateral view.

less conspicuous. Some hair is lost along the mid-dorsum in what is probably a partial spring molt. By early August the winter pelage has replaced the thin partially molted hair. The animal winters in this subadult pelage and develops the first adult coat with the spring replacement the following year.

DISCUSSION

It is significant that an animal which is active only a few months of the year should display two molts in this short period of time. The rapid processes of hair replacement are doubtless an adaptation to the unusual climatic conditions of the far north. Apparently *Spermophilus undulatus* is the only New World ground squirrel to show this type of molting. Comparisons with Old World forms have not been made. According to Hansen (1954) many ground squirrels of southern distribution have two annual molts but northern members have only one. This species does not conform to this general statement. It is also atypical when compared with the other ground squirrels because molting is most erratic and definite molt lines are rare. A few individuals do not molt twice each year but retain the winter coat all season. Many specimens taken in July or August are in complete winter pelage. These animals have either completed a winter molt or have skipped the spring molt.

The badly depilated areas of some animals may possibly be explained, in certain cases, by observations on captive animals. Some squirrels have been observed to pull hair from cage mates and this may cause considerable hair loss. Whether this happens in the wild is not known. Apparently this behavior is not sexual in nature since it occurs equally in males and females.

The partial spring molt of juveniles occurs later in the year, paralleling the growth processes. The excessive wear of the pelage of the young is an index of their early strenuous activity. Animals in capivity show continuous molting from late May to late October. This suggests that hair loss or replacement is occurring in some degree during the entire period of summer activity in this ground squirrel.

SUMMARY

Spermophilus undulatus kennicotti has a spring and winter molt annually which occur during the five months of summer activity. The molting patterns for spring, winter and juvenal molts are described. Spring molt proceeds posteriorly in definite sequences but in an erratic manner and with definite molt lines. The winter molt progresses without molt lines, is rapid, and occurs in reverse order from that of the spring molt. The first juvenal molt occurs somewhat later in the season than the spring molt of adults and is only a partial hair replacement. Molting in this ground squirrel apparently differs from that of all other North American forms of this genus in that two molts are completed in such a short period of annual activity.

This research was supported by the United States Air Force under Contract AF 18 (600)-843, monitored by the Arctic Aeromedical Laboratory, Alaskan Air Command, Ladd Air Force Base, Alaska.

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THE UTERUS MASCULINUS OF *CASTOR CANADENSIS*

BY C. H. CONAWAY

The remarkably large bicornuate uterus masculinus of the European beaver, *Castor fiber*, has been noted by various workers since attention was first directed to this structure by Brandt and Ratzeburg (1829). More recently it has been described by Hinze (1950) and Freye (1953) who comment that the American beaver, *C. canadensis*, apparently does not possess a male uterus. They probably base this conclusion upon Tullberg's (1899) account of the complete absence of a uterus masculinus in the single *C. canadensis* he dissected. Actually, such a structure has been noted briefly by Ely (Appendix "A" in Morgan, 1868).

The purpose of this study is to describe the gross and microscopic anatomy of the uterus masculinus of *Castor canadensis*. The extent of individual variation and correlations with the reproductive cycle are also reported.

METHODS

Reproductive tracts of 17 male beavers, 2 male embryos, and 2 females were collected from carcasses obtained from fur trappers in Western Montana from January to April, 1953. The appearance of the uterus masculinus in five other specimens was noted, but the reproductive tracts were not preserved. At the time the carcasses were received, they were weighed and an estimate of the age of the specimens was based on this criterion using Osborn's (1953) categories. The weights and corresponding age classes were as follows: under 25 lbs., one year; 25 to 35 lbs., two years; over 35 lbs., adult. Since the specimens were taken just prior to or during the breeding season, the youngest animals were approximately one year old. The entire reproductive tract was removed and fixed in A.F.A. (alcohol-formal-acetic). The animals had been dead for varying periods of time before they were received and fixation was, therefore, often poor. Dr. H. W. Mossman provided one additional male specimen (No. 20) collected in Wisconsin during the spring of 1952.

The fixed tracts were photographed; then measurements and notes concerning the gross morphology were taken. Testes and seminal vesicles were removed and weighed. Sample histological sections of testis, seminal vesicle and uterus masculinus from each individual were cut at 8μ and stained in a modified Schorr stain. Serial sections of the prostatic urethra of three specimens

were also prepared. Microscopic measurements were made by an ocular micrometer. Tabulated measurements (Table 1) are averages of 10 separate readings.

RESULTS

Gross anatomy—The morphology of the uterus masculinus in the specimens examined was so highly variable that each specimen was unique. Some form of rudiment was always grossly visible in the area dorsal to the prostatic urethra and base of the bladder and medial to the vasa deferentia. A specimen showing symmetrical development (No. 20) will be described first and the remainder compared with it.

The uterus masculinus of specimen No. 20 is a bicornuate structure fusing caudally into a single median tube (Plate I, 1). The horns are symmetrical tubes 1 mm. in diameter and 14 mm. in length. They are parallel to the vasa deferentia and attached to them throughout by delicate mesenteries 2 to 5 mm.

TABLE 1.—*Summary of data from individual reproduction tracts*

SPECIMEN NO.	DATE	TESTES WT., GM.	SEMINAL VESICLE WT., GM.	HEIGHT UT. EPITH., μ	HEIGHT GLAND EPITH., μ	THICKNESS MYO., MM.	THICKNESS STROMA, MM.	DORSAL VENTRAL DIAM., MM.	LENGTH CORPUS, CM.	LENGTH RT. HORN, CM.	LENGTH LEFT HORN, CM.	NO. CYSTS	NUCLEI IN 150 μ^2	AGE*
1	30 Jan.	18	18	12	13	.15	.10	.60	0	5.0	4.5	0	30	A
2	6 Mar.	9	4	20	16	.20	.50	1.20	0	0.6	0.7	4	75	2
3	15 Mar.	6	1	22	22	.10	.10	.55	1.1	1.5	2.4	0	60	1
4	18 Mar.	18	20	15	16	.50	.50	3.30	0	3.1	3.2	3	24	A
5	15 Mar.	16	14	17	21	.30	.35	1.20	3.2	0.9	0.9	1	33	A
6	12 Apr.	18	22	13	15	.25	.30	1.50	0	1.0	1.0	1	21	A
7	12 Apr.	11	16	14	14	.45	.45	2.40	0	1.0	1.3	2	32	A
8	15 Mar.	3	2	18	20	.20	.20	1.20	0.2	1.2	1.1	0	60	1
9	30 Mar.	13	35	12	12	.40	.25	2.70	0	0.9	0.5	1	13	A
10	5 Mar.	12	12	18	21	.10	.25	1.35	2.4	0	3.0	2	56	2
11	5 Mar.	16	34	9	9	.15	.25	1.35	2.6	3.1	2.0	0	19	A
12	15 Apr.	15	13	16	16	.20	.20	1.20	0	3.3	1.9	0	20	2
13	30 Jan.	‡	1	†	†	.10	.15	.70	1.0	0.5	0.6	0	38	1
14	15 Mar.	10	12	14	20	.35	.35	1.50	0.5	0.9	0.8	3	27	A
15	6 Mar.	11	11	†	†	.10	.15	.75	2.4	0	1.1	1	60	2
16	20 Mar.	18	27	17	14	.25	.40	1.85	0.4	0.8	0.8	1	31	A
17	15 Mar.	5	15	14	16	.10	.25	.60	2.1	0.7	0.7	0	28	2
20	Jan.-Mar.	‡	1	15	16	.20	.35	1.65	1.5	1.4	1.4	0	49	1

* A = adult, 3 years or more; 1 = one year old; 2 = two years old.
† Preservation poor; measurement not taken.
‡ Testes not preserved.

in length. The cornua meet in the midline at the level of the base of the urinary bladder and cephalic ends of the ampullae. The corpus thus formed extends caudad 15 mm. It is bounded laterally by the ampullae, ventrally by the neck of the bladder and prostatic urethra, and dorsally by the seminal vesicles. The latter are united by connective tissue except at their cephalic ends so that the caudal extent of the corpus cannot be seen without dissection. The lumina of the cornua continue into the corpus as parallel ducts for approximately 12 mm. and then merge to form a single canal which continues caudally 3 mm. before ending blindly. At the point of fusion of the lumina, the entire structure tapers very rapidly and terminates in a thread of tissue which cannot be followed caudally beyond the level of the ejaculatory ducts.

The cephalic ends of the cornua appear to end abruptly but close examination shows that a thread of tissue continues along the medial border of each vas deferens toward the testis. The threads cannot be followed in specimen No. 20 since the vasa deferentia were cut and the testes were not preserved. In all complete tracts the threads extend along the vasa deferentia to the tail of the epididymis. At that point they either merge with the connective tissue or extend across the caput epididymis to the testis and fuse with the tunica albuginea.

The other specimens are similar but usually asymmetrical with one uterine horn or the corpus being short or absent (Table 1 and Plate I, 2–4). The canal in the corpus always ends blindly and does not open into the urethra. There is no indication of a prostatic utricle on the colliculus. Isolated cysts of 1 to 2 mm. in diameter frequently occur at any point along the filament extending toward the testis. The blood supply of the uterus masculinus is from branches of the deferential artery.

The five specimens which are not tabulated and for which preserved tracts are not available had minimally developed rudiments. Threads were visable along the vasa deferentia and several cysts appeared in each individual. Distinct cornua or corpora did not occur.

Microscopic anatomy.—The major aspects of the histology of the uterus masculinus of the beaver are similar to those in the female uterus (Plate I, 5). Individual variation is restricted to the amount of development of the various regions.

The endometrial epithelium is simple columnar with individual variation in the height of the cells (Plate I, 6–9). In the lower corpus region of some specimens, the epithelium is cuboidal with a few basal cells. Uterine glands similar to those of the female are present in all specimens. The number and size of the glands, however, vary in individual specimens. They are always fewer in the corpus than in the cornua. Lumina of glands appear to contain secretion products but only a trace of such material is found in the uterine lumina. The stroma is cellular and comparable to the immature female uterus in some specimens while in others it is highly collagenous. The myometrium is composed of an outer longitudinal stratum and a thicker inner circular

stratum of smooth muscle. Individual variation in the thickness of the myometrium occurs.

Serial sections of the prostatic regions of three animals were studied to determine microscopically the caudal extent of the uterus and the structure of the colliculus. In the 12-cm. embryo the median tube terminates between the vasa deferentia at the level of the base of the bladder. A strand of connective tissue extends caudally a short distance and merges into the connective tissue dorsal to the bladder at the level of the internal openings of the ureters. Caudal to this level the only rudiment of the female duct system is seen on the colliculus seminalis where a mid-dorsal evagination 0.3 mm. in depth lies between the openings of the ejaculatory ducts. The diverticulum is lined with the urogenital sinus type of stratified epithelium similar to and continuous with that of the urethra. There is no evidence of any anatomical juncture between this prostatic utricle and the uterus masculinus.

There is no suggestion of a prostatic utricle in either of two yearling specimens studied. The uterus masculinus of No. 20 terminates caudally in a strand of connective tissue dorsal to the urethra and about 10 mm. cephalic to the level of the openings of the ejaculatory ducts. In No. 3 a narrow canal lined with cuboidal epithelium extends caudally as far as the level of the junction of the seminal vesicles with the ejaculatory ducts.

Cyclic variation.—Analyses were made to determine if variation in the uterus masculinus was correlated with the reproductive cycle. The weight of the seminal vesicle was taken as an index of reproductive development. Comparisons of several morphometric histological characters with seminal vesicle weights were made by calculating regression equations and the significance of the regression. These data are summarized in Table 2.

Highly significant results were obtained when regressions of seminal vesicle weight on the height of uterine epithelium, height of uterine gland epithelium and number of nuclei in a 150μ square of stroma were calculated. These three values decrease rather uniformly as seminal vesicle weight increases. As an example, the regression of seminal vesicle weight on height of uterine epithelium

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1. Uterus masculinus (U) of beaver No. 20. V = vas deferens; S = seminal vesicle; P = prostate; B = urinary bladder. Approximately × 1¼. **2.** Uterus masculinus (U) of beaver No. 4. The short cornua and corpus are enlarged and cystic. Approximately × ⅓. **3.** Uterus masculinus (U) of beaver No. 3. Asymmetrical cornua and a short corpus are present. Approximately × 1⅓. **4.** Uterus masculinus (U) of beaver No. 12. Cornua are continuous across the midline and a corpus is absent. Approximately × 1⅓. **5.** Cross section of uterus masculinus of No. 20 through the right horn. Note the uterine glands and general similarity to rodent uteri. Approximately × 27. **6.** Section of endometrium of one-year-old animal No. 8. The epithelium is high and the stroma cellular with little connective tissue. Approximately × 460. **7.** Section of endometrium of adult No. 7. The epithelium is lower and less cellular than that shown in **6.** Appriximately × 460. **8.** Section of endometrium of adult No. 14.The epithelium and stroma are of the adult type. Approximately × 460. **9.** Section of endometrium of one-year-old animal No. 3. Compare the high epithelium and cellular stroma with **7.** and **8.** Approximately × 460.

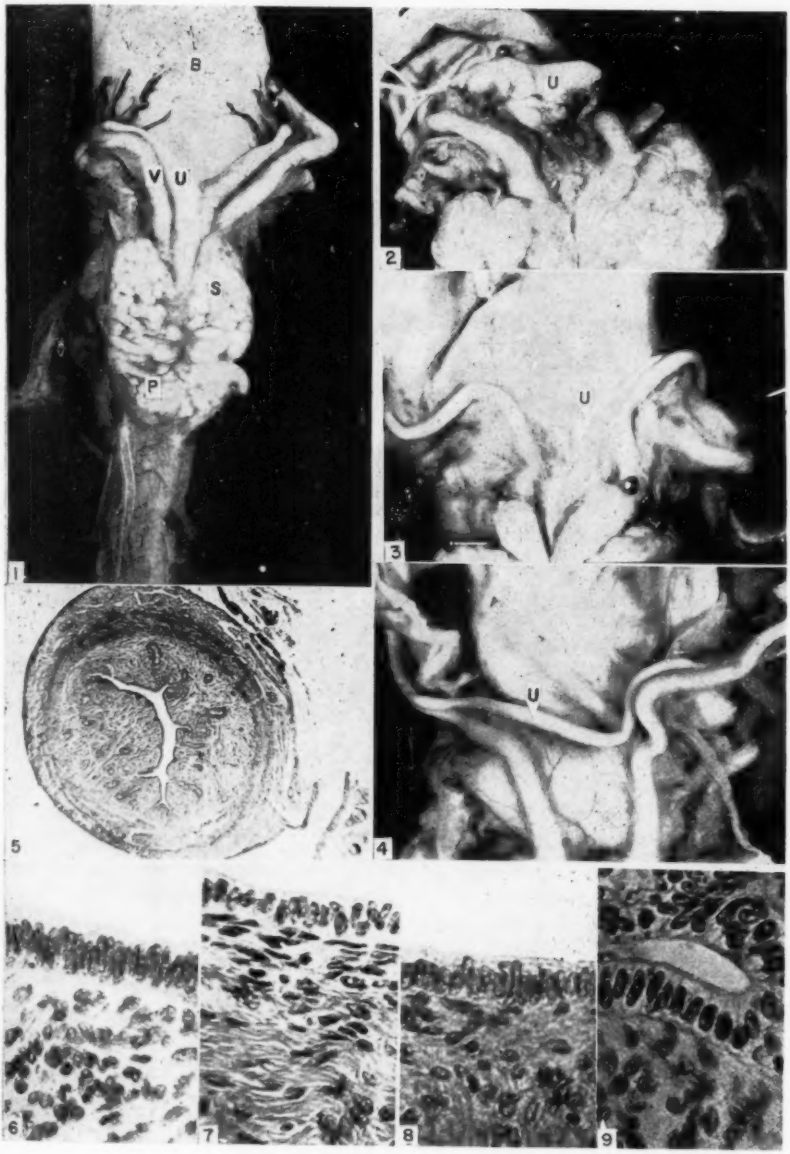

PLATE I (legend opposite)

is also presented graphically in Fig. 1. The regression of seminal vesicle weight on testis weight was calculated for comparison. It is interesting to note that the *P* value here was 0.5 as compared with less than .01 for the three endomtrial measurements.

No evidence for correlation was obtained when regressions of seminal vesicle weight on each of a second group of measurements were computed. The *P* values of the regressions of thickness of myometrium, dorsal-ventral diameter of the uterus masculinus, and thickness of the stroma were all between 0.3 and 0.5. This group of measurements concerns characters which most directly relate to the gross size of the uterus and they indicate that variation in the gross anatomy probably does not correlate with seminal vesicle weight.

DISCUSSION

The embryological origins and homologies of heterologous duct rudiments in the male have long been disputed. Much of the confusion is attributable to similar uncertainties regarding the origin of the female vagina. It now seems apparent that in many species the vagina is largely derived from the urogenital sinus (Zuckerman, 1940; Raynaud, 1942*b*). Careful studies of the development of the rabbit vagina, however, have shown that in this species the müllerian ducts make a major contribution to the vagina (Jost, 1947; Carr, 1953). Thus it seems that variation in the origins of the vagina occurs between species.

Various origins are described for small diverticula on the colliculus of the male, such as the primate prostatic utricle. In man this diverticulum is stated to arise from the caudal portion of the müllerian ducts (Meyer, 1909; Vintemberger, 1926) or the urogenital sinus (Vilas, 1932). The epithelium of the utriculus in other primates shows considerable species variation. It may be a single layer of cuboidal cells without glands, or it may be glandular and "uterine" in appearance (Zuckerman and Parkes, 1935). These epithelia respond to estrogens with either squamous hyperplasia on glandular proliferation (Zuckerman and Parkes, 1936*b*). Zuckerman (1940) has empha-

TABLE 2.—*Regressions of seminal vesicle weights (x) on uterus masculinus measurements (y)*

y	REGRESSION EQUATION	$s_{y \cdot x}$	*r*	*P*
Stroma index	$y = 55.69 - 1.2661x$	12.30	−.74	.01†
Myometrium thickness	$y = 19.88 + .2039x$	12.48	+.28	.30
Stroma thickness	$y = 27.30 + .0696x$	13.13	+.09	.50
X-section diameter	$y = 12.31 + .1251x$	7.47	+.12	.20
Height uterine epithelium	$y = 18.84 - .2235x$	2.31	−.73	.01†
Height uterine glands	$y = 20.15 - .2503x$	2.58	−.73	.01†
Testis weight	$y = 7.23 + .3231x$	3.85	+.57	.05*

* = 95 per cent confidence level.
† = 99 per cent confidence level.

sized that in either sex the urogenital sinus epithelia react to estrogens by undergoing squamous hyperplasia, and müllerian epithelia by glandular proliferation. Therefore, it appears that the primate utriculus may vary between, and possibly within, species as to its origin.

Evidence suggestive of the origin of heterologous duct rudiments in other species is based largely upon the gross and microscopic anatomy of the structures in adult males. Weber's (1846) study and Leuckart's extensive survey (*in* Todd, 1852) of the comparative gross anatomy of duct rudiments, show that the form and amount of tissue persisting is highly variable. Weber (1846) regarded all duct rudiments as homologous with the uterus while Leuckart (*in* Todd, 1852) emphasized that both uterine and vaginal components were always present. A more plausible interpretation is that either vaginal or uterine portions may occur alone or that both may be present or both absent. Duct rudiments in cattle, sheep and goats are not typically connected with the urethra and histologically they are entirely uterine (Swoboda, 1929). Small diverticula on the colliculus of the prostatic utricle type are often purely vaginal in character, as in the guinea pig (Hutt, 1927), many primates (Zuckerman and Parks, 1936*b*), and some carnivores (Swoboda, 1929). These diverticula also show both vaginal and uterine portions. The horse has a large (5–7 cm) diverticulum which clearly is vaginal in the caudal and uterine in the cephalic part (Guyon, 1939).

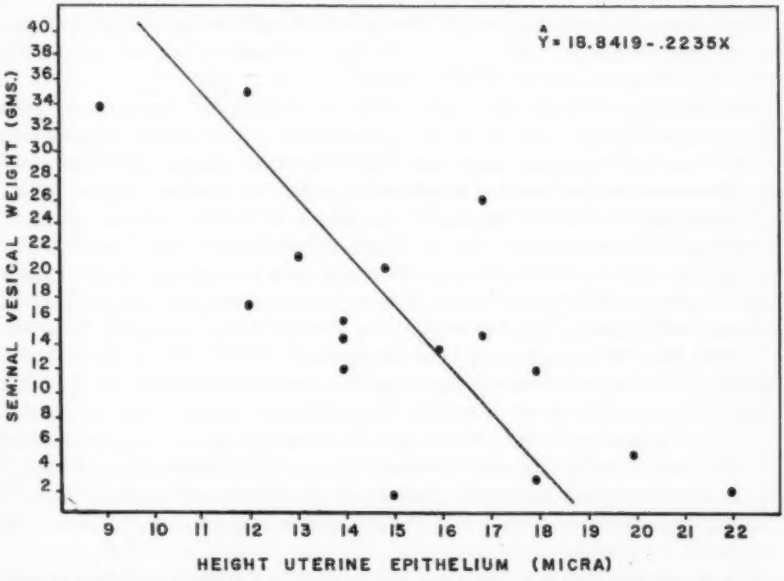

FIG. 1.—Regression graph of seminal vesicle weight on height of epithelium of uterus masculinus.

Studies of the prostatic region of *Mus* (Raynaud, 1942*a*) and of *Microtus arvalis* (Delost, 1951) show that in embryos there is a prostatic utricle of urogenital sinus origin and a uterine segment of müllerian origin. Isolated cysts along the vas deferens similar to those found in adult beavers occur in some embryos of *Microtus arvalis* (Delost, 1951).

The gross and microscopic anatomy of the duct rudiments in *Castor canadensis* are so clearly uterine that there seems no doubt that the structures are of müllerian origin. In the specimens studied the uterus ended blindly a variable distance cephalic to the level of the colliculus. Ely (*in* Morgan, 1868) indicated this was also true in the individual he examined. Such a condition would be expected if the caudal müllerian cords degenerate early as Vilas (1932) describes in the human. Failure of the urogenital sinus epithelium to invade along the degenerating müllerian cord would result in a cystic müllerian rudiment. The only indication of a typical prostatic utricle in the beaver was seen in one embryo. This structure is minute and lined by sinus epithelium. The müllerian ducts fuse and terminate considerably cephalic to this level. The distinctness of sinus and müllerian epithelia in the rabbit embryo has been noted by Carr (1953), who states, "The histological appearance of the epithelium indicates its origin."

Cystic müllerian rudiments have been reported in several species. They normally occur in cattle, sheep and goats (Swoboda, 1929). In 132 cattle with müllerian rudiments, only cystic structures were found (Skoda, 1917; Swoboda, 1929). The prominent rudiment of the horse may end blindly or may open into the urethra (Swoboda, 1929). It is not stated whether a vaginal segment is present in the cystic uterus in these species.

The descriptions of the uterus masculinus of *Castor fiber* suggest that there may be some difference from that of *C. canadensis*. Many reports indicate that an opening into the urethra occurs and imply that there is little individual variation. However, the total number of animals actually described may be very small.

Original descriptions of the uterus masculinus of *Castor fiber* are given by Brandt and Ratzeburg (1829), Weber (1846), Chatin (1874) and Freye (1953). In each case the description seems to be based upon a single specimen. Brandt and Ratzeburg (1829) figure a very large symmetrical uterus masculinus which they say ends blindly. The figure given by Weber (1846) is similar; however, he stated that the uterus opens into the urethra. Chatin (1874) described a remarkable uterus with cornua extending along the vasa deferentia to the testis where they terminated in a swollen and recurved vesicle. He stated that the vesicle was covered by a thick layer of striated muscle. The cornua met posteriorly as a single tube which entered the urethra between the ejaculatory ducts. The description and figure given by Freye (1953) are similar to Weber's (1846); however, Freye does not indicate whether or not the uterus communicates with the urethra.

The descriptions of the uterus masculinus given by Hinze (1950), Weber (1927), Meisenheimer (1921–30) and Leuckart (*in* Todd, 1852) seem to be

based entirely upon Weber's (1846) work. The account given by Owen (1868) cannot be considered since both the species described and the extent of original observation seem questionable.

The original descriptions indicate that all four specimens of *Castor fiber* had larger uteri than any seen in *C. canadensis*. The cornua were always symmetrical and in two of the four specimens the uterus opened into the urethra. These descriptions suggest that although the uterus masculinus of the European beaver shows some individual variation, it is generally better developed than that of *C. canadensis*.

Extensive individual variation in the form and amount of heterologous tissue persisting in the adult has been noted in all other species for which large series have been examined. Vilas (1932) found much variation in size and point of entry into the urethra of the human prostatic utricle. Similarly, Skoda (1917) found that of 115 cattle examined, 82 showed müllerian rudiments. These were usually single small cysts but as many as three cysts were found in some individuals. Cysts varied in size, shape and position with one example of a median type with short horns. Swoboda (1929) also noticed great variation in cattle, sheep, goats and horses, but apparently less in the smaller prostatic utricle of swine, dogs and cats.

The evidence obtained in this study suggests that the cellularity of the stroma, and height of uterine and glandular epithelia regress when reproductive activity increases. However it should be noted that all of the animals studied were taken during the reproductive season. Those showing little or no reproductive activity at that time are of younger age classes. Thus a simple maturative regression quite apart from the sexual status would also explain the data obtained. It seems much more probable, however, that the changes described are controlled by the reproductive cycle. A study of adult animals from the nonbreeding season would help to establish the correct interpretation.

Heterologous duct tissues of many species respond to castration or hormonal treatment under experimental conditions. The height of the utricular epithelium of two normal guinea pigs was 20–25μ and in two castrates it lost its glandular appearance and was only 10–11μ (Hutt, 1927). Androgens produce slight stimulation of the epithelium of castrate guinea pig utriculus (Laqueur, 1936). Estrogens cause a pronounced mucous hyperplasia especially in the immature or castrate but also evident in the intact adult (Courrier and Cohen-Solal, 1936).

Androgens have no effect on the prostatic utricle of the macaque (Zuckerman and Parkes, 1936*a*). The prostatic utricle of many primates, however, responds to estrogens by undergoing keratinization or glandular hyperplasia depending upon whether it is formed from sinus or müllerian epithelium (Zuckerman and Parkes, 1936*b*). The caudal vaginal segment of the horse uterus masculinus is similar in both normal and castrates while the anterior uterine segment may be slightly more active in the normal than in the castrate animal (Guyon, 1939). Guyon suggested that the testicular estrogens of the horse are either inactive or inactivated by testosterone and thus not stimulatory in the intact animal.

Evidence of normal cyclic variation in the uterus masculinus is limited. Vintemberger (1926) states that changes in the human prostatic utricle occur at puberty. Prior to puberty the epithelium is stratified but after puberty it is columnar with basal cells and appears similar to the prostatic epithelium. The prostatic utricle of *Elephantulus* undergoes marked seasonal changes fluctuating with the prostate (Stoch, 1954). She reports that the epithelium of the utricle in the non-breeding male is only half as high as that of the breeding male. In contrast to these reports Swoboda (1929) specifically states with regard to cattle, sheep and goats: "Im allgemeinen kann gesagt werden, dass wie in makroskopischer so auch in histologischer Hinsicht das Lebensalter oder die Kastration Keinen Unterschied ergibt."

The above findings are somewhat conflicting but in general it seems that, with regard to heterologous duct tissues in the male, (1) estrogens are stimulating in all species studied with the maximum effect produced in the absence of male hormone; (2) androgens produce slight stimulation or have no effect; (3) castration produces regressive changes or has no effect; (4) normal cyclic variation is reported in only a few species and in these the maximum development correlates with maximum reproductive levels. It may be noted that those instances where stimulation is produced by androgens or is correlated with reproductive activity all involve prostatic utricula of almost certain urogenital sinus origin.

The endometrium of the beaver uterus masculinus shows definite regressive changes correlated with increasing reproductive activity. This seems to be the first report of such inverse variation. A valid explanation of the physiological controls cannot be given at this time. Possibly feminizing hormones may be present and stimulate the uterus in the immature male. When high levels of testosterone are present, the feminizing hormones are either not produced, are inactivated, or their action is blocked.

A problem of considerable interest is the cause of the normal persistence of prominent müllerian rudiments such as those found in the male beaver. The work of Jost (1953) would suggest that in mammals a factor from the fetal testis is responsible for regression of the müllerian ducts in the male and that there is a limited sensitive period over which this factor must act. He finds the area most sensitive to inhibition is the portion of the müllerian ducts nearest to the testis while the caudal segment is the most insensitive and persistent. In the beaver it is a segment presumably near the caudal end of the müllerian duct which most frequently occurs. Perhaps, then, in this species testis inhibition is not completely effective because of low levels of the inhibiting substance or because the action begins too late.

ADDENDUM

Two additional adult specimens were obtained after this manuscript was submitted to the editor. The reproductive tract of one adult male was collected by E. Provost on August 24, 1956, in Massachusetts. The second adult was

obtained October 8, 1956, from A. Brohn of the Missouri Conservation Commission. Testes weights of both specimens were 10 grams; seminal vesicle weights were 1 and 3 grams. Histological examination showed that the testes of both animals had regressed. The seminal vesicle weights were the lowest recorded and indicate minimal stimulation. The histology of the uterus masculinus of both specimens was similar to that of adult males taken in the breeding season. Apparently there is no seasonal cycle in the uterus masculinus of adult beavers. Regression occurs with the onset of sexual maturity and the uterus masculinus remains in the regressed condition even when the adults are reproductively inactive. This would be expected unless feminizing hormones were present during the non-breeding season.

SUMMARY

The uterus masculinus of the American beaver is highly variable in form. The most symmetrical development seen in 25 specimens examined was a bicornuate uterus with cornua 14 mm. long and a median corpus 15 mm. long. In other specimens the cornua were asymmetrical or absent and in five cases only connective tissue threads were found medial to the vasa deferentia. The uterus masculinus was always cystic and did not open into the urethra. The histological structure was similar to that of the female uterus. The height of the uterine epithelium, the height of the glandular epithelium and the cellularity of the stroma decreased as the weight of seminal vesicles increased. The regressions of seminal vesicle weight on these groups of data were highly significant while regressions on thickness of stroma, thickness of myometrium and diameter of the uterus masculinus were not significant.

ACKNOWLEDGMENTS

I am indebted to R. M. Miller, Deputy Game Warden, Montana State Fish and Game Commission for his aid in obtaining material. Specimens of female reproductive tracts were obtained from H. W. Mossman and P. L. Wright. Dr. Mossman gave helpful comments regarding this study.

This work was supported by a grant from the University of Missouri Research Council.

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ADRENOCORTICAL ACTIVITY IN TWO MEADOW VOLE POPULATIONS

By Charles D. Louch

The object of this study was to observe the relation between population density and adrenocortical activity, as measured by adrenal weights and blood eosinophil levels, in free-living populations of the meadow vole, *Microtus pennsylvanicus*. The study was initiated to test the hypothesis presented by Christian (1950) that high population density constitutes a stress factor eliciting a response from the adrenopituitary systems of individuals making up the population and thus brings about the occurrence of the General Adaptation Syndrome of Selye (1946).

The study was begun in the late summer of 1952 and extended through the fall of 1953. Two widely separate areas were chosen after inspecting a large number of areas in the vicinity of Madison, Wisconsin, for evidences of high meadow vole populations. One area, called the Mud Lake Area, had a very high population in the fall of 1952, while the other, the Hammersley's Marsh Area, had a low to normal population at this time.

This research was carried out in the University of Wisconsin, Department of Zoology, with the aid of grant number G-3497 (C-C2) from the National Institutes of Health of the U.S. Public Health Service, and with aid from the Wisconsin Alumni Research Foundation. At this point I would like to thank Dr. J. T. Emlen and Dr. R. K. Meyer for their advice and encouragement in the conduct of this research; helpful suggestions and friendly criticisms were also offered by numerous members of the Zoology Department.

STUDY AREAS

The Mud Lake Area is located in Dunn Township near the town of McFarland, Wisconsin, and is 1 mile due west of Mud Lake. It consisted, at the time of study, of about three acres of grass marsh which became very wet during periods of high precipitation. The area was bordered on the west by a corn field while the other three sides were bordered by additional grass marshland. About ½ mile to the east the grass marsh ran into a cattail-sedge marsh which in turn bordered the lake. Both southward and northward the marshland continued for approximately ¼ mile before giving way to cultivated fields. The area was grazed regularly during the summer when it was dry enough to allow cattle on it. The vegetation, mainly grasses, appeared to maintain itself well under the moderate grazing which occurred, and provided ample food and cover for a good field mouse population.

The Hammersley's Marsh Area, about two acres, is located on the Madison Beltline about half a mile from the southwest limits of the city of Madison, Wisconsin. It was bordered on the west by the highway and on the east by a small lake. The area closest to the road was vegetated by a thick growth of grass which was mowed periodically by the Highway Department. About 75

feet in from the road the grass gave way to cattails and sedges which extended to the lake. The level of the lake varied greatly during the year, being very high during the spring and early summer and very low during the late summer and fall. At its high level most of the cattail area was flooded and water extended up to within 100 feet of the road, while at low level the edge of the water was over 100 yards from the road. The cattail and low grassland area formed a 50- to 100-yard-wide strip completely around the lake giving an extensive vole habitat of which the study area was a small part. Evidences of voles were found in this entire area by the methods described below.

METHODS

Population measurements.—The initial population density of each area examined was estimated by the frequency of occurrence of fresh vole droppings and grass cuttings, using a modification of a method described by Hayne (1950). In the present study a straight line was paced across the area, a search for vole sign being made at ten-pace intervals. The percentage of the total number of stops at which fresh vole sign was found provided an indication of the population density of the area. This method was rough but adequate for the purposes of this study. The Mud Lake area yielded mouse sign at 98 per cent of the stops, indicating the highest population density encountered in the search, while the Hammersley's Marsh Area yielded sign at 20 per cent of the stops, indicating an average population for that type of habitat and time of year—November, 1952.

During the course of the project changes in the population of each area were determined roughly from the number of animals caught per trap hour. There was undoubtedly a large error in this method, but it appeared accurate enough for the purpose of this study.

Trapping the mice and taking blood.—The study involved live-trapping mice and using their blood for making eosinophil counts. The methods used were designed to minimize the effects of trapping and handling upon the blood eosinophil levels.

The trap lines were run once each month, excluding January and August of 1953. Trapping was continued in each area only long enough in each month to obtain a statistically ample number of animals. Therefore, the length of time spent trapping varied somewhat from one month to another depending upon how rapidly the animals were caught. All the trapping was done during the day, from about 3 to 6 PM. As I have shown (Ph.D. dissertation, Univ. Wisconsin, 1955), there is no significant difference in the blood eosinophil levels of *Microtus* at different times of the day between 9 AM and 9 PM; therefore the time of trapping and blood taking should have had no influence on the data obtained.

Blood eosinophil levels were used as one criterion of adrenocortical activity since it has been demonstrated that increased adrenocortical activity is accompanied by lower blood eosinophil levels and that this relationship is specific

(Speirs and Meyer, 1949). Blood eosinophils of *Microtus* were found to show this inverse relationship (Louch, *loc. cit.*); therefore this criterion of adrenocortical activity could be utilized in the present study. The eosinophil counts in this study were made using a method described by Speirs and Meyer (1949).

Twenty-four fiber-board box traps of a drop-door treadle design were set in a line through each area at approximately ten-pace intervals. Peanut butter or rolled oats were used as bait. After the traps were set the line was patrolled constantly so that mice could be removed as soon as trapped and transferred to a heating chamber in order to dilate the blood vessels of the tail. The heating chamber, a box with fiber-board sides and top and an aluminum bottom, was placed on a stand over an alcohol lamp. After being heated for five minutes, the mice were removed from the chamber and tail blood was taken and prepared for counting. The prepared blood was held in the pipettes until it could be returned to the laboratory where the counts were made not more than five hours later. This practice of holding the blood for several hours before counting had no effect on the eosinophil counts obtained; immediate counts yielded a mean value of 43.00 cells/mm.^{3} of blood, while delayed counts yielded 43.67; the calculated "*t*" value was 0.0364, and P*t* 0.9.

Autopsy of mice.—After blood was taken from the animals they were autopsied in order to determine their reproductive condition. The adrenals were removed and weighed on a spring-torsion balance and the weights recorded as milligrams per gram of body weight. Increased adrenal weight indicates an increased adrenocortical activity (Selye, 1946).

The reproductive condition of the males was determined by the position of the testes, the length and appearance of the seminal vesicles, and the presence or absence of macroscopically visible tubules in the cauda epididymis. In sexually active mice the testes are scrotal and from 10 to 15 mm. long; the seminal vesicles are enlarged and turgid, with round lobes; and the tubules of the cauda epididymis are clearly visible macroscopically (Jameson, 1950; Hamilton, 1941).

The reproductive status of the females was determined on the basis of whether the vulva was perforate or not, and upon the width of the uterus. The ovaries were also examined for size and presence of corpora lutea, which are prominent throughout pregnancy (Hamilton, 1941). Sexually active mice were characterized, when not pregnant, by a perforate vulva, a uterus more than 1 mm. wide, and prominent ovaries, usually with corpora lutea. Inactive mice have an imperforate vulva, a uterus less than 1 mm. wide, and small ovaries with no corpora lutea.

RESULTS AND DISCUSSION

The results of the monthly eosinophil counts are shown in Table 1 where it may be seen that the eosinophil counts of the Mud Lake population were significantly lower than those for the Hammersley's Marsh population during November and December of 1952, but not for the rest of the study period.

TABLE 1.—*Mean monthly eosinophil counts (cells per mm.³ of blood) for both areas, based on all animals of 18 gm. or more regardless of whether sexually active or inactive*

MONTH	MEAN EOSINOPHIL COUNTS				MEAN DIFF.	"t"	Pt
	Hammersley	n	Mud Lake	n			
1952							
Nov.	82.12	7	21.60	15	60.52	4.223	0.01
Dec.	93.81	6	38.32	8	55.49	5.960	0.01
1953							
Feb.	109.48	6	104.60	7	4.88	0.230	0.50
Mar.	91.76	9	120.04	5	28.28	1.805	0.10
Apr.	93.80	7	122.25	6	28.46	1.836	0.10
May	160.74	13	142.91	6	17.83	0.282	0.50
June	129.53	7	97.44	5	32.09	1.325	0.30
July	112.51	7	126.30	5	13.79	0.228	0.50
Sept.	147.70	6	163.33	6	15.63	0.385	0.50
Oct.	178.80	9	178.33	6	0.47	0.008	0.50
Nov.	208.00	10	150.00	6	58.00	1.997	0.10

Table 2 shows that, in the Mud Lake Area, the mean eosinophil level for November and December of 1952 was significantly lower than the mean level for the rest of the year. This difference was not significant in the Hammersley's Marsh Area. The abrupt rise in eosinophil levels that occurred in the Mud Lake Area in February accompanied the marked population decline that had occurred by that time (Fig. 1). In both areas there was a gradual rise in eosinophil levels through the summer and fall of 1953 until the highest levels were achieved in November of 1953.

Table 3 shows the statistical analysis of the male adrenal weight data. The mean adrenal weight in the Mud Lake Area for November and December of 1952 was significantly higher than the average for the Hammersley's Marsh Area during the same period, while there was no difference between the means for the rest of the study period. In each area the mean adrenal weight for November and December of 1952 was significantly higher than the mean for the rest of the year. The adrenal weights of the female mice were not used here because the onset of reproductive activity in the spring was accompanied by a marked increase in the female adrenal weights from a mean of 0.211 in

TABLE 2.—*Comparison of the eosinophil levels (cells per mm.³ of blood) in the fall of 1952 with those for the rest of the study period in both areas*

AREA	MEAN EOSINOPHIL LEVELS		D.F.	DIFF.	"t"	Pt
	Fall	Rest of period				
Mud Lake	27.42	131.30	72	103.88	8.841	0.01
Hammersley	87.12	143.78	86	56.66	0.677	0.90

the fall and winter of 1952–53 to a mean of 0.474 mg. per gm. of body weight in the spring and summer of 1953.

The above data seem to indicate that there was some factor or combination of factors which brought about increased male adrenal weights in both areas and decreased eosinophil levels in the Mud Lake Area during the fall of 1952.

The factors which might possibly have brought about the results described above could have been meteorological in nature, such as temperature or humidity, or biotic, such as changing population levels or variations in the amount of food or cover.

A lack of food and/or cover probably was not effective as a stress factor since the vegetation was heavy in both areas throughout the period of the study. The population density for the two areas, as determined on the mouse-per-trap-hour basis, is shown in Fig. 1. From this figure it is apparent that the high population density in the Mud Lake Area accompanied, and may have been an important factor in bringing about, the significantly lower eosinophil counts and higher adrenal weights observed in this area during the fall of 1952.

However, the significantly higher adrenal weights in both areas during the fall of 1952 would seem to indicate some rather widespread agent as being a possible contributing mechanism. Data from the records of the U.S. Weather Bureau at Madison show that September and October of 1952 were very dry with a total precipitation of 0.68 in., 5 in. below normal for this time of year. This represents the worst autumn drought ever recorded in the Madison area, and this drought condition resulted in the two study areas being unusually dry. The first part of November was warm and dry; precipitation beginning on the

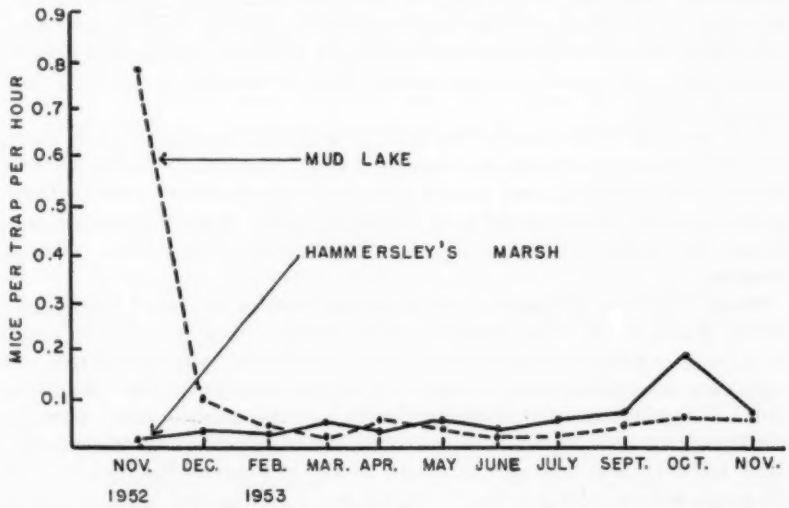

FIG. 1.—Population density of voles in each month based on number of captures.

TABLE 3.—*Statistical analyses of adrenal weight data for male mice; mean adrenal weights in mg. per gm. of body weight*

DATES	MEAN ADRENAL WEIGHTS		DIFF.	D.F.	"t"	Pt
	Hammersley	Mud Lake				
Nov.-Dec. 1952	0.194	0.230	0.036	19	16.363	0.01
Feb.-Nov. 1953	0.152	0.145	0.007	42	0.350	0.90
AREA	NOV.-DEC. 1952	MARCH.-NOV. 1953				
Hammersley	0.194	0.152	0.045	28	2.091	0.05
Mud Lake	0.230	0.145	0.065	33	5.636	0.01

16th brought ground moisture back to almost normal levels. The period in November during which trapping was carried out was part of the drought period. The total precipitation for September and October, 1953, was 2.76 in., which is still below normal but considerably higher than for the same period in 1952. It is thought that the unusual dryness of the fall of 1952 may have constituted a stress factor for animals such as *Microtus* which normally live in rather damp habitats.

Thus the significantly higher male adrenal weights for both areas, and the somewhat lower eosinophil levels at Mud Lake during the fall of 1952, may be partly attributed to this drought condition. The temperatures for this period were relatively mild and so probably played no part in the phenomena observed. However, the significantly lower eosinophil levels and higher adrenal weights in the Mud Lake Area as compared to the Hammersley's Marsh Area indicate that some local factor, probably high population density, acted as an added stress in the former area. Therefore the drought condition and the high population density may have had a cumulative effect in eliciting increased adrenocortical activity.

It is possible that reproductive activity held the eosinophil levels down somewhat during the spring and summer of 1953. Figure 2 shows the per cent of the mice caught in each month that were reproductively active. These observations are similar to those of Hamilton (1941) that free-living populations of the meadow vole are usually reproductively active from March through October.

Female mice are polyestrous and the young females may mate successfully at four weeks of age. Thus females born in the spring may be sexually active in the same season. An estrous cycle occurs immediately after parturition and some mice are capable of conceiving five or six days after parturition (Hamilton, 1941). The conclusion that adult females are probably sexually active throughout the spring and summer is supported by the high percentage of reproductivity active mice at this time, as shown in Fig. 2. Many of the females used for counts were in early pregnancy and this may have resulted in a lowering of the eosinophil levels in these animals. The fact that the adrenals of the females

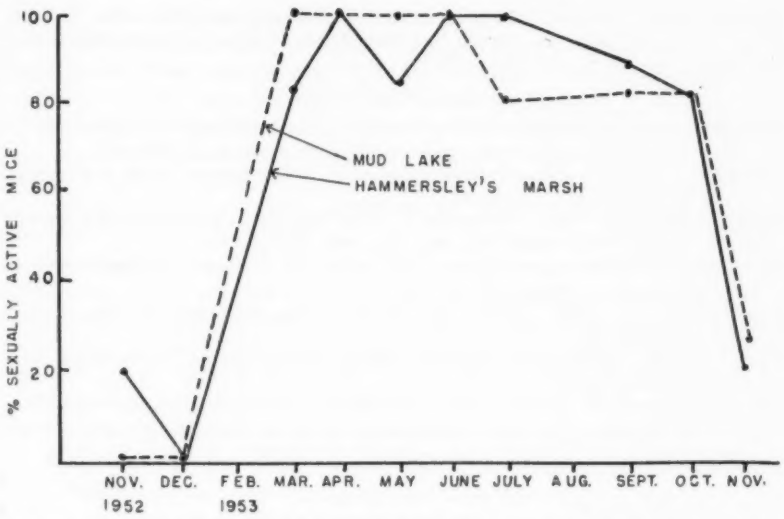

FIG. 2.—Reproductive activity of voles weighing 18 grams or more in each month.

were enlarged during the spring and summer, as mentiond above, supports the idea that reproductive activity may increase adrenocortical activity to some extent. Bourne and Suckerman (1940) found a change in the adrenal weights of female rats correlated with the estrous cycle.

Male meadow voles may become sexually active at approximately five weeks of age (Hamilton, 1941) and individual males probably remain sexually active throughout the spring and summer.

Thus sexual activity may have had some effect upon the eosinophil data obtained in this study; precisely what effect cannot be stated with the information presently at hand.

SUMMARY

The relationship between population density and adrenocortical activity was studied in two free-living populations of meadow voles using blood eosinophil levels and adrenal weights as the criteria of adrenocortical activity. The Mud Lake Area had a high population density during the fall of 1952 and a low population density during the rest of the study period, while the Hammersley's Marsh Area had a low to normal population throughout the period of the study, November, 1952, to November, 1953.

Two factors appeared to be acting to bring about the greater adrenocortical activity observed in the fall of 1952 in both areas. One of these, the drought conditions of that fall, appeared to act in both areas to bring about increased adrenocortical activity. The other factor, high population density, was present only in the Mud Lake Area and appeared to increase the adrenocortical activity of the mice in that area to significantly higher levels than in the Hammersley's Marsh Area. It is suggested that the drought conditions and the high population density present in the Mud Lake Area in the fall of 1952 may have had a cumulative effect on adrenocortical activity resulting in significantly higher adrenal weights

and lower eosinophil counts than in the Hammersley's Marsh Area at that time. The data indicate that high population density is a stress factor eliciting increased adrenocortical activity, as suggested by Christian (1950).

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ECOLOGY OF THE SWAMP RABBIT IN GEORGIA

BY CHARLES E. LOWE

All four species of rabbits of the genus *Sylvilagus*, namely *S. floridanus*, *S. aquaticus*, *S. palustris* and *S. transitionalis*, which occur in eastern North America are found in Georgia. The four species are separated ecologically either by habitat or range differences. *Sylvilagus aquaticus* occurs on the floodplains and bottomlands of the Piedmont and the Appalachian Valley of Georgia, while *S. palustris* occupies a similar habitat in the Coastal Plain and also the coastal marshes. *Sylvilagus floridanus*, the common cottontail, has a statewide distribution but lives on the uplands, while *S. transitionalis* is found only at high elevations in the mountains.

Gray (1867) separated the two species of semiaquatic rabbits (*aquaticus* and *palustris*) from the cottontails (*floridanus* and *transitionalis*) and placed them in the subgenus *Tapeti* on the basis of differences in cranial characteristics as well as in habits. Two subspecies of *S. aquaticus* have been described but only *S. a. aquaticus* is found in Georgia. *S. aquaticus littoralis* occupies a narrow belt of swamps and marshes along the Gulf Coast from Bay St. Louis, Mississippi, west through Louisiana to Matagorda Bay, Texas. As presently understood the over-all distribution of *aquaticus* and *palustris* is shown in Fig. 1 (insert).

This paper deals principally with the swamp rabbit, *Sylvilagus aquaticus aquaticus*, which is commonly called "canecutter" or "buck" in Georgia. This is probably the least known of the eastern rabbits. It is considered a first-class game animal which is well worth conserving. If a full understanding of the requirements of this subspecies is to be had, more information on its life

history and ecology is needed. Also, the presence of closely related species provides an opportunity to evaluate the importance of Gause's rule (i.e., no two closely related species occupy the same ecological niche; see Odum, 1953, p. 170) in determining the distribution of species in nature.

This study was designed (1) to determine from field observation throughout the year the general behavior, habitat requirements, and life history of *aquaticus* in the Piedmont region, (2) to clarify ecological relationships with *palustris* and *floridanus*, and (3) to establish from the study of collected specimens the morphological features which characterize *aquaticus* populations in Georgia.

This study was carried out while the author held a Wildlife Conservation Fellowship made possible by a grant to the University of Georgia from the Georgia Game and Fish Commission, and was directed by Dr. Eugene P. Odum. A number of individuals aided in field work, especially Dr. James Jenkins, Neil Hodgson, Tatum Daley, Nick Mudick, Bill Leach, and Henry Robert.

This is a contribution from the Department of Zoology, University of Georgia and the Georgia Game and Fish Commission. The material here presented is contained in a thesis submitted for the degree of Master of Science, University of Georgia.

METHODS

In September, 1951, a study area was selected along the Oconee River and Sandy Creek floodplain just north of the city limits of Athens, Georgia, in Clarke County (Fig. 2). Besides being close to the University, the area was considered typical *S. aquaticus* habitat and seemed to contain a relatively large population (ascertained from reports of local hunters and observation of rabbit scats in the area).

The Oconee River study area was used for trapping and observation. Conventional wooden rabbit traps with fall-type doors, and with either solid or screened backs, were tried but with little success. Corn, apples, sweet potatoes, turnips, carrots, and vanilla flavoring were used as baits. While eleven cottontails were caught only four canecutters were trapped and only one was caught a second time. Vanilla flavoring was used in all successful canecutter captures.

Useful home range data for the swamp rabbit were obtained through the employment of trained beagles which were persistent in trailing the rabbit across streams, ponds, and through brush and vines, yet which were not fast enough to drive the rabbit from its customary home range. The "slow dog" technique also enabled the writer to observe the behavior of rabbits and to become acquainted with individuals. A boat was used at high water to check the location of canecutters on the study area. At flood times a good census was possible because the animals took refuge on floating logs, crotches of trees, or dry knolls, and could be easily located.

Specimens were obtained for laboratory study from various areas (but not the above study area) in several counties. Collecting was done with the aid of dogs. Black-and-tan raccoon dogs were used with the beagles on several

collecting trips to "tree" the rabbits when they ran into hollow trees or holes in the ground. Forty-three specimens of *aquaticus* were collected together with a larger number of cottontails. A few *palustris* were also taken where the range of this species adjoins that of *aquaticus* (Fig. 1). Standard body measurements (body length, tail, hind foot, fore foot, and ear notch) were taken on each specimen and study skins were prepared in most cases. Standard cranial measurements as diagrammed by Orr (1940) were made with a vernier caliper. All preserved specimens have been deposited in the University of Georgia collection.

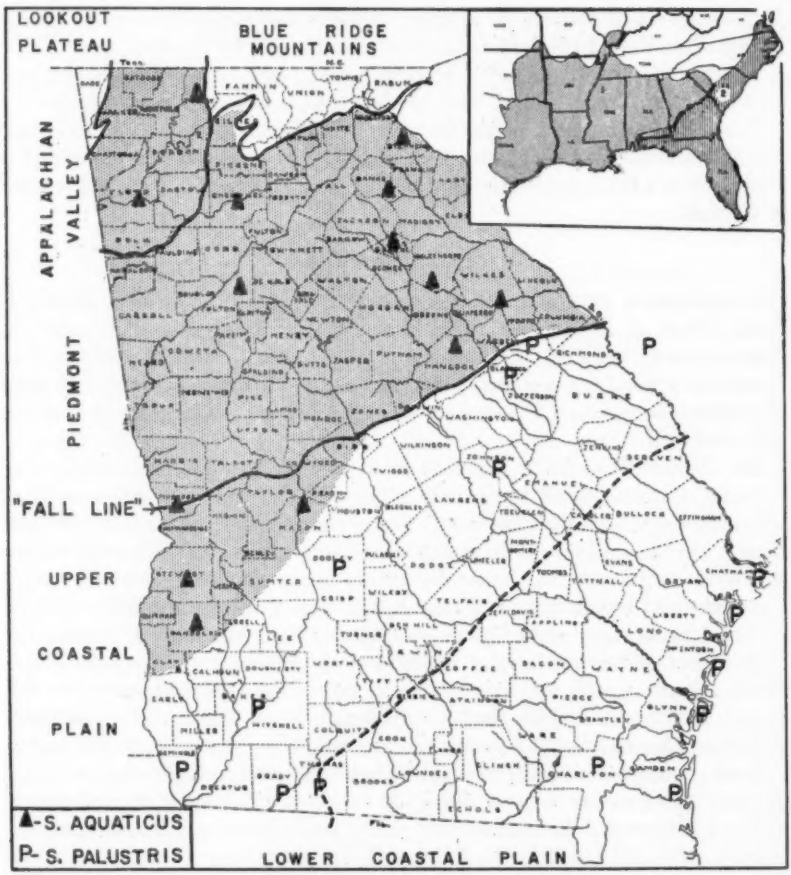

FIG. 1.—Distribution of the swamp rabbit and marsh rabbit in Georgia as currently understood. Insert (modified from Hall, 1951) shows over-all distribution of *S. aquaticus* (1) and *S. palustris* (2).

RESULTS OF FIELD OBSERVATIONS

General behavior.—The canecutter inhabits floodplains of rivers or creeks of the Piedmont and is not seen very far from such habitats except occasionally during the breeding season. Large, slightly splayed toes with sharp nails aid the canecutter in moving about in its habitat of water and soft mud. Its gait varies with circumstances, sometimes resembling a walk, sometimes a hop, and

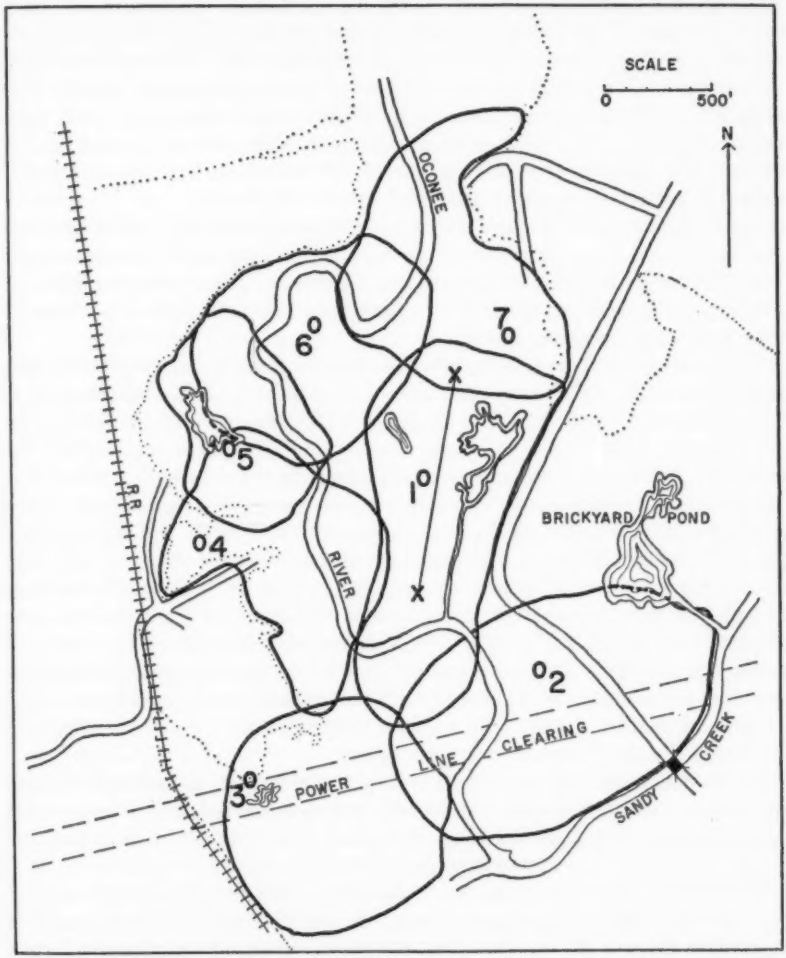

FIG. 2.—Fall and winter home ranges (heavy lines) of seven swamp rabbits as indicated by the use of dogs. Numbered ovals indicate points where individuals were most often flushed. The two X's indicate points where No. 1 was trapped on two different dates. The extreme limits of the floodplain are shown by dotted lines.

sometimes a slithering, crawling motion, especially as it cautiously leaves one of its tunnels in the vegetation. Since canecutter habitats vary in the amount of cover, water, and open spaces, disturbed rabbits do not react identically in different areas.

The swamp rabbit in common with other species frequently escapes detection by remaining perfectly still as it sits in its form. Often it does not move until the vegetation within a foot of its position is disturbed. On several occasions, rabbits remained quiet until they were almost stepped upon. Their coloration blends so well with brown leaves or grass that they may be easily overlooked by an observer. On hot, dry days, the study area was carefully hunted with dogs several times without "jumping" a single rabbit, whereas on cool, rainy days, as many as three rabbits were jumped on the same area in an equal amount of time. I am not certain whether animals "sit closer" on hot days or whether dogs are less able to pick up the scent.

Sylvilagus aquaticus builds its forms in places where it can detect intruders and have access to vegetation or water for escape. Tops of old stumps covered with vegetation, low crotches of trees, logs, Japanese honeysuckle tangles, cane patches and open grassy places in the floodplain were observed to be common form sites for this aquatic rabbit.

The canecutter is an accomplished swimmer. On five occasions two men paddling a boat on the study area were unable to overtake a swimming canecutter. One individual, when closely pursued by dogs, was seen to dive into the water from a bank several feet high; keeping only its head partially above the surface it drifted with the current to the opposite shore several hundred feet downstream. Swamp rabbits can often outsmart even the best dogs by going from islet to islet and then remaining almost submerged in the water near a log or brush until the danger is past. Again, animals were observed to escape by "laying a backtrack" at the water's edge and then floating downstream. In quiet or standing water, the canecutter was observed using a swimming motion similar to that of a dog. Young canecutters just out of the nest take to the water readily. On two occasions very young canecutters were observed swimming a distanct of 50 yards between islands in the Brickyard Pond (Fig. 2). Canecutters shot in the water remain afloat for a time indicating that air trapped in the fur exerts a buoyant effect.

A common habit of *S. aquaticus* is that of defecating on logs and stumps. By checking defecation sites at intervals, it was estimated that eleven pellets per defecation was about average. I believe a reliable index of population numbers based on a scat count might be worked out.

Cottontails, when being removed from a box trap, usually remain quiet if their eyes are covered, but canecutters strike out viciously with their hind feet even when the eyes are covered. The only way to prevent being scratched when removing them from a box trap or hollow log is to grasp the hind feet with one hand, then slide the other hand around the front legs and head. The rabbit, if held stretched between the two hands, will then remain quiet.

Sometimes a canecutter grits its teeth and appears as if about to bite the holder. This action seems to be a relief mechanism or merely a bluff since none of the animals handled made a real attempt to bite.

When first handled by man or caught by a dog, the canecutter emits a series of loud screams, similar to but much louder than those of the cottontail. When startled in the field, the rabbit freezes in a rigid position and attempts to remain inconspicuous, but does not make a sound. There is no evidence that the voice has any significance in mating or social relations generally.

Like most rabbits, the canecutter appears not to notice a person who is perfectly still unless the wind is blowing toward the rabbit. When pursued by dogs, the rabbit stops frequently to look around, listen, and twitch the nose, testing the air for odors. When laying backtracks, the rabbit sniffs the ground occasionally as if to determine whether or not it has been past a certain point before going on in another direction. A male canecutter, which was later shot and found to be in breeding condition, was observed following fresh tracks of another rabbit.

Nesting.—Few canecutter nests or nesting sites have been reported in the literature. Goodpastor and Hoffmeister (1952) reported a nest at Reelfoot Lake in Tennessee. The nest was in a heavy weed patch and contained four young. Strecker and Williams (1929) found a nest containing two young under a fallen branch in Bowie County, Texas. Local sportsmen reported finding canecutter nests in bottomland hay fields. The number of young reported varied from two to four.

Only one nest was found by the author during his study. It was located on a semi-island below the Oconee River Dam at Athens in the recently cleared right-of-way of a power line. On March 21 three young, with their eyes open and with complete pelage, were snugly fitted into a depression which was 6½ inches wide and 3 inches deep. The depression was lined with fur plucked from the mother's belly, but not with grass as is the nest of the cottontail in this locality. A dense canopy of honeysuckle shielded the nest so well that it probably would not have been found had not the area been cleared. Young from another nest were brought to the author but no description of the nest was obtained.

Natality.—The canecutter has been credited with from four to six young per litter and with two litters per year but little direct evidence substantiates so large a number per litter (Hamilton, 1943). Table 1 shows the data obtained from pregnant canecutters and cottontails collected during the present study. Also shown are the number of young found in nests.

Since litter size in rabbits in general is known to vary according to age of the female and the season of reproduction, the average of 2.6 per litter is only suggestive. Northern cottontails are generally reported to average 4 to 5 per litter (Trippensee, 1936; Hamilton, 1943; Haugen, 1942) but Bruna (1952) has shown that litter size may be smaller southward.

Mortality.—A few canecutters, while traveling between river drainages, are

killed by automobiles and occasionally a few are caught by the fast dogs of a pack. However, neither of these are important causes of mortality as they are in the case of the cottontail. Man with his automatic shotgun and large pack of dogs might drastically reduce the canecutter population in a small area, but the cutover swamps with their tangles of cane, Japanese honeysuckle, briers and hardwood offer the canecutter an excellent refuge. As indicated below, the habitat itself appears to be the most important limiting factor. (Table 1.)

TABLE 1.—*Number of embryos in pregnant specimens (E) and number of young found in nests (N) in the field*

S. aquaticus			*S. floridanus*		
Date		Number of young	Date		Number of young
March 21	(*N*)	3	March 25	(*E*)	2
April 25	(*E*)	2	March 30	(*E*)	3
June 30	(*N*)	4	March 30	(*E*)	3
Sept. 1	(*E*)	3	April 4	(*E*)	3
Sept. 4	(*E*)	1	May 3	(*E*)	4
			May 13	(*N*)	2
Average		2.6	May 20	(*N*)	5
			June 3	(*N*)	2
			Aug. 1	(*E*)	2
			Average		2.9

Habitat selection.—This study offered an opportunity to test Gause's principle in connection with the canecutter and cottontail. During the winter and early spring months when water levels were high the major part of the canecutter's habitat in the study area was not occupied by cottontails. Cottontails could be found around the edge of the swamp and on the ridges, but they did not go beyond the edge of the flooded area. The utilization of cane and emergent aquatic plants as food by the canecutter but not by the cottontail also separates the two species ecologically. During the summer the canecutters, in general, remain close to water. Although the cottontails ranged into the drier parts of the swamps at this season, no range overlap was observed in most areas. Where the slopes adjacent to the swamps lacked adequate cover for cottontails, some overlap occurred since cottontails were observed using the cover available in the swamps.

Home range.—Figure 2 shows the plotted maximum home range of seven canecutters on the study area during the fall and winter of 1951, as determined from observed routes taken by the animal when pursued by dogs. Also shown are the sites within each range where single rabbits were most often observed or jumped from forms. The animal in range 1 was the only one captured twice in a box trap, and the points of capture are indicated. It will be noted that all seven of the consistently occupied ranges contained either a floodplain pond or a section of river, or both. After home ranges were plotted on a map, the

areas were computed with a planimeter. The average for the seven ranges was 18.9 acres (Table 2).

TABLE 2.—*Maximum size of fall and winter home ranges of swamp rabbits as mapped in Fig. 1*

RANGE NO.	AREA, ACRES
1	22.8
2	27.5
3	18.7
4	16.1
5	11.0
6	18.0
7	18.4
Average	18.9

Several times, while the floodplain was inundated and only a few knolls were above water, a boat was utilized to check the spatial relationship of rabbits. For example, midway between the two points of recapture for canecutter No. 1 (Fig. 2) is a small knoll usually above high-water mark. Each time a boat was used, a single rabbit, presumably the same rabbit, was seen on the knoll. In addition, other rabbits were consistently observed close to points where they were usually jumped by dogs. Thus, observations made at times of high water served to substantiate observations made at other times.

No direct evidence of territoriality was obtained; only one rabbit was observed to occupy a given home range. The overlap of ranges during the fall and winter was not great. Also, when three rabbits were killed by hunters, other rabbits from areas adjoining the study areas took their places. This replacement procedure occurred four times near the power line right-of-way where sparse cover made rabbits more vulnerable to hunters. Thus, it would appear that an occupied area is avoided by other rabbits.

Population density.—Since the study area comprised about 131 acres, and contained an average of seven rabbits, the population density during the fall and winter of 1951–52 was approximately 5.6 rabbits per 100 acres of bottomland. An insight into the relationship between cattle grazing and numbers of swamp rabbits was provided when a portion of floodplain adjoining the study area was fenced and stocked with cattle. As the cattle ate and trampled vegetation, more time was required to jump the rabbits and fewer rabbits were found in the area. Canecutters were still plentiful in the undisturbed part of the swamp. Removal of the cattle and subsequent vegetational growth probably raised the carrying capacity of the area because the number of rabbits jumped per hunting trip increased. It is probable that suitable habitat is the most important limiting factor for the swamp rabbit in the well-drained Piedmont region where bottomlands are not extensive.

Growth of a captive specimen.—A young swamp rabbit weighing 472 gms., captured on June 30, 1952, was kept in captivity for a year. After about four months the captive had developed the typical adult pelage and weighed 1345 gms. which is about the minimum weight of sexually mature rabbits collected in the field (see Table 3). At this time the captive was estimated to be between 5½ and 6 months old. At one year of age it weighed 1482 grams.

On several occasions the captive canecutter was observed drinking water. The animal sipped water from a pan and then removed the remaining drops of water from its mouth and vibrissae with its tongue. The large quantities of water required by this animal were probably due, in part, to the dry nature of the prepared diet.

TABLE 3.—*Weights of adult swamp rabbits and cottontails from the Georgia Piedmont*

SPECIES, SEX	NUMBER	MEAN WGT., gms.	STANDARD DEVIATION	RANGE
S. aquaticus, ♂♂*	24	1895	64.1	1432–2345
S. aquaticus, ♀♀*	12	1951	277.7	1332–2385
S. floridanus, ♂♂†	26	1106	78.2	973–1299
S. floridanus, ♀♀†	25	1170	112.8	964–1382

* Difference between sexes not significant ($t = 0.42$; $p = 0.70$).
† Females significantly heavier than males ($t = 2.34$; $p = .025$).

STUDY OF COLLECTED SPECIMENS

External appearance.—*Sylvilagus aquaticus* is a large, yellow-brown, big-headed rabbit. It may be distinguished from *S. floridanus* by its larger size, more robust head, mule-like ears (they tend to be floppy), splayed feet, and heavier toenails. Usually the darker coloration of the soles of the hind feet and the more slender tail are evident (Table 3). The coloration of the hind feet appeared to vary according to the humic acid content of the water in the natural habitat. Young canecutters are grayish-brown with dusky underparts, including the underside of the tail, in contrast to the white underparts of the adult. When they leave the nest the pelage is coarse or rough in contrast to the sleek appearance of the adult.

Weights.—Data on weights of 36 swamp rabbits and 51 cottontails are summarized in Table 3. Females with large embryos were not included. Female cottontails were significantly heavier than males, as reported by Bruna (1952), but no sexual difference was evident in *aquaticus*. However, the number of females in the sample was small. Hunters have reported swamp rabbits weighing up to 8 pounds but the largest which I obtained weighed 2385 grams or 5.35 pounds. It will be noted that there was very little overlap in the weights of the two species; the smallest *aquaticus* which was judged to be sexually mature weighed about the same as the largest *floridanus* specimen.

Measurements.—Body and cranial measurements of *aquaticus* are summarized in Tables 4 and 5. Differences between sexes were tested satistically for all measurements and in no case was the difference considered significant (*P*

TABLE 4.—*Body measurements of 43 adult swamp rabbits (S. aquaticus); differences in sexes not significant*

MEASUREMENT	MEAN, mm.	STANDARD DEVIATION	RANGE
Body length	444	22.3	268–498
Tail length	72	8.9	57–93
Hind foot	104	4.0	93–111
Fore foot	55	2.5	46–59
Ear notch	73	2.4	68–77

greater than 0.05); hence all adults have been lumped in the tables. When compared with the sample of 49 cottontails all measurements of *aquaticus* were significantly greater except for the diameter of the external auditory meatus and the width of the nasals which were not significantly different in the two species. Differences between *aquaticus* and *palustris* will be discussed below.

DISTRIBUTION AND RELATIONSHIPS

The distribution of the swamp rabbit (*aquaticus*) in Georgia, as currently understood, is shown in Fig. 1. In the eastern half of the state *aquaticus* extends down to the "Fall Line" (the physiographic feature separating Piedmont from Coastal Plain), but in the western part of the state it is found well below this line at least as far south as Randolph county (Harper, 1929). The marsh rabbit (*palustris*) is found in the remainder of the state, the range of the two species in a jigsaw puzzle. In Georgia there is definitely no gap between the ranges of the two species, as shown in the maps in Hamilton's book (1943) and in Hall's monograph (1951).

In working the counties on both sides of the eastern portion of the Fall Line the author found what was judged to be either one or the other species, never both in the same locality. No difference in habitat selection was evident.

TABLE 5.—*Cranial measurements of 37 adult swamp rabbits (S. aquaticus); differences in sexes not significant*

MEASUREMENT	MEAN, mm.	STANDARD DEVIATION	RANGE
Basilar length	68.1	2.4	60.9–72.3
Zygomatic breadth	40.5	1.0	37.1–42.4
Zygomatic arch length	38.7	1.6	35.0–42.1
Postorbital construction	20.5	2.1	18.1–29.2
Length of nasals	37.4	2.6	32.5–40.8
Width of nasals	15.6	1.0	13.6–18.6
Length of molar series	17.0	1.0	12.2–18.2
Diameter external auditory meatus	4.6	0.3	4.1–5.4
Breadth of brain case	26.7	0.8	24.8–27.9
Length palatal bridge	17.0	1.0	12.2–18.2

Indeed, it would appear that the habitat of both species depends on what is available in the way of wet lands. Thus, *aquaticus* may be found both in coastal marshes and wooded interior swamps in the Gulf region, while in the Atlantic region *palustris* may also be found in coastal marshes or wooded swamps many miles inland (see also Nelson, 1909; Blair, 1936; Carr, 1939; Sherman, 1939; Svihla, 1929; Tompkins, 1935).

While the author felt that he was able to place specimens in either one or the other species category, it was apparent that specimens of *palustris* from the Upper Coastal Plain were intermediate in size and coloration between typical *palustris* of the coastal strip and *aquaticus* of the Piedmont. Coastal *palustris* are easily distinguishable from *aquaticus* in being smaller, darker above and below (including underside of tail) and in having smaller, more naked feet. Cranial differences appear to be more quantitative than qualitative. Specimens from Glascock County near the Fall Line (Fig. 1), however, were similar to typical *aquaticus* in color of upperparts and only slightly darker below. Upper Coastal Plain *palustris* specimens were also intermediate in size as shown in Table 6. These data and observations suggest that the two species may interbreed along the junction of the ranges, or even that they are conspecific (with well-marked races or "semispecies"). However, before any such conclusions can be made a much larger series of specimens must be studied. Equally important, field observations are needed to determine if competition plays a role in keeping the populations apart.

TABLE 6.—*Comparison of measurements (in mm.) of S. aquaticus and S. palustris in Georgia*

MEASUREMENT	*S. aquaticus* from Piedmont (from Tables 4, 5)	*S. palustris*	
		From Upper Coastal Plain (9 specimens)	From Lower Coastal Plain (6 specimens)
Body length	444	396	388
Tail	72	45	36
Hind foot	104	94	92
Ear (notch)	73	63	60
Basilar length of skull	68	63	60

SUMMARY

1. Behavior, home range and population density of swamp rabbits, *Sylvilagus aquaticus*, were investigated on a 131-acre study area, and specimens were collected over a wide area to clarify relationships with *S. floridanus* and *S. palustris*.

2. The swamp rabbit is more elusive and harder to observe and trap than the common cottontail; the two species occupy different habitats with little overlap. The use of trained dogs proved the best technique for observation of home range and behavior.

3. Home ranges averaged about 19 acres and density was about 5.6 per 100 acres during fall and winter. All home ranges contained water which was freely utilized for escape.

4. The breeding season extends at least from March to September. Litters averaged 2.6 (2.9 for cottontails). Only one nest was found.

5. Weights, body and skull measurements are tabulated. Differences between sexes were

not significant for any measurement. Weights averaged 1960 grams (1140 for cottontails collected from same region) with maximum of 2385 (5.4 lbs.).

6. The Fall Line marks the approximate boundary between the range of *aquaticus* and *palustris* in eastern but not in western Georgia. One but not both of these species was found in all localities investigated. However, upper coastal plain *palustris* specimens were somewhat intermediate in color and size between *aquaticus* and *palustris* from the coastal strip pointing up the need for further study of relationships between these very closely related species.

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SUMMER OBSERVATIONS ON MOOSE BEHAVIOR IN ONTARIO

By Antoon de Vos

Various aspects of the biology of moose in Ontario were studied during the summers of 1952, 1953 and 1955. The present paper concerns itself with vocal and social behavior, reactions to disturbances, food habits, and the influence of weather on movements. Data on moose movements, sex and age ratios, antler development and shedding of winter hair have been presented elsewhere (de Vos, 1956).

An area in the center of the Chapleau Crown Game Preserve, seldom visited by humans, was chosen for this study since it is preferable that observations be carried on without undue disturbance to the moose. Studies were restricted to Little Missinaibi Lake (Fig. 1), ideal for extensive moose observations because its numerous arms make possible frequent extended trips by canoe. The lake is generally shallow, providing large quantities of aquatic vegetation in its various sections. The local moose population has been at or around carrying capacity level for some years, as evidenced by heavy browsing pressure which has existed on various palatable trees and shrub species close to the lake for some time.

It should be emphasized that the behavior data were collected as a sideline to the data already reported upon. It is fully realized that more fact-finding should be undertaken in order to come forth with statements, based on data of a more quantitative nature.

Methods.—Daily trips were made by canoe along various arms of the lake from a base camp. To avoid undue disturbance of the animals, no one arm, except the one on which this camp was situated, was visited more frequently than once every third day. Several tent camps were used at sites suitable for observations and overnight trips were made to such camps. Normally the canoe was manned by two, but sometimes by three observers. Daily records were kept on the length of the period during which observations were made, the area covered, maximum-minimum temperatures, sky conditions, and periods of rainfall.

Whenever moose were observed, data were recorded on time of observation, age, sex, location, and special characteristics of individuals. During 1952, 1953 and 1955, 7 × 50 binoculars were used; during 1955, a 25 × telescope supplemented observations with binoculars. Whenever possible, moose were not approached within their flushing distance to avoid the possibility of alarming them to the extent of causing them to make abnormal movements during succeeding days.

The field work was under supervision of the author, who was assisted each year by two students and occasionally by personnel of the Department of Lands and Forests.

Vocal behavior.—It is generally supposed that moose are vocal only during the rutting season, when various grunts, whines or bellows are uttered. However, we heard moose call during the entire summer. No calls were ever heard by the author during winter and spring. Various noises were recorded. Actually, the various calls except for a whine should only be differentiated on the basis of the circumstances under which they were produced. At least the author is unable to notice much difference.

The most commonly heard call is an alarm call, which is produced by adults of both sexes. It is a short, hoarse sound, resembling a noise somewhat between the barking of a dog and the mooing of a cow, uttered when a moose appears to be alarmed. The mouth is apparently not opened to produce this sound. While a moose will generally stop "barking" after the

initial disturbance, on occasion it will continue to do so for some time (at least 10 min.). The first alarm call of the season was recorded on June 19, 1955; others were heard during the balance of that month, and during July and August. The alarm call of a bull seems more guttural than that of a cow and somewhat resembles the "grunt" or "burp" produced during the rutting season. Dr. W. H. H. Gunn has a tape-recording of this call on file.

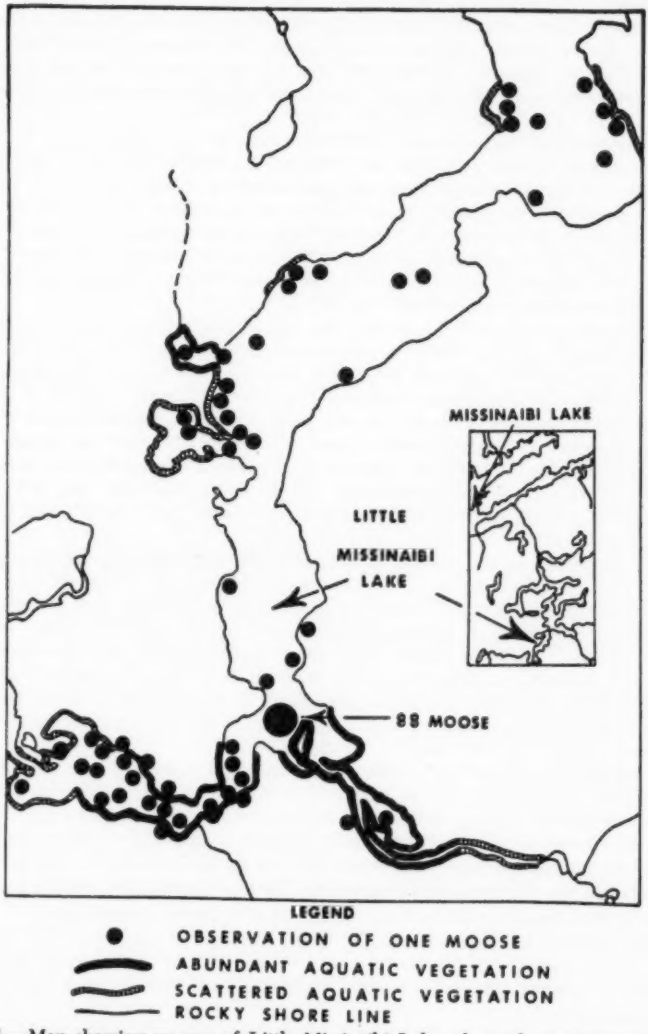

FIG. 1.—Map showing an arm of Little Missinaibi Lake where observations were made in 1952, 1953, 1955 and 1956. The correlation between moose occurrence and abundance of aquatic vegetation is clearly indicated. Insert shows the entire lake.

A high, plaintive whine is uttered by calves and yearlings, apparently to attract the cow. On three different occasions two calves and one yearling were heard producing these sounds while feeding with their mothers. All three repeated their whines many times. The cows did not show any obvious reactions to these whines. On three other occasions, calves reacted to disturbances before cows did, and whined. One cow subsequently grunted. In another instance a two-year-old bull uttered a single whine.

When a cow wishes to attract her calf she may utter a low, short grunt, similar to the alarm call. Once a calf was observed to come out of the brush after its mother had grunted.

Social behavior.—Apart from a close association between a cow and her calf (calves) and often her yearling(s), and also between a cow and a bull during the rutting season, moose do not appear to be very sociable animals.

Most of the moose which are seen in close proximity to each other during the summer seem to congregate in relatively few sites because of a high availability of aquatic food. Sometimes as many as a dozen moose are concentrated in a large marshy bay where the aquatic vegetation is abundant. Figure 1 shows the correlation between the occurrence of moose in one of the arms of Little Missinaibi Lake and the presence of aquatic vegetation. Relatively few moose are observed where aquatics are absent or scarce and where the shores are rocky. The largest number of observations was made where considerable aquatic vegetation was concentrated in shallow bays (Fig. 1).

If moose congregate in a suitable feeding spot, one notices that individuals generally arrive and leave separately and pay little or no noticeable attention to each other. Occasionally two animals seem to associate with each other for a time. For instance, an old bull and a two-year-old bull were observed to be feeding and moving together for a period of two days. However, the old bull was observed eight days later at the same location without the young one. A younger animal associating with an older one is called a "satellite" by Altman (1956).

Generally speaking, bulls do not seem to develop much interest in cows before early September. However, on August 19, 1951, a bull and a cow were seen feeding close together for at least 15 minutes, and appeared to have more than a casual association with each other.

During the winter several animals of different ages and sexes may form loose bands. Normally such groups consist of two to four animals, but sometimes half a dozen or more may move and feed together. It is not known how long a bull stays with a cow after the rutting season or how tightly knit winter associations are. At any rate, groups of two to six moose are not uncommon during the winter, especially when they are "yarding up" because of considerable snow on the ground. Adult bulls are sometimes seen moving along in a widely dispersed group. On an airplane flight from Geraldton to Sioux Lookout in 1949, for instance, I noticed such a group of a dozen bulls, all traveling in the same direction, which covered about ½ mile or more.

Many yearlings stay with their mother during most of the summer, and possibly longer than that. The cow pays attention to them as illustrated by an observation made on July 27, 1955. A cow and her twin yearlings were first observed as they crossed a bay. The bull yearling stayed close to the cow, but the female yearling lagged behind, feeding on aquatics. The cow and the bull yearling waited on the shoreline for her and, when she finally arrived, the cow pushed her with her head into the bush. The number of yearlings that were running with cows varied from about 25 to 50 per cent of the total yearling population.

Behavior which might be interpreted as "play" was noticed only once. On August 17, 1951, a cow moose and her calf were observed chasing each other through a willow swale for about ten minutes. They were running back and forth, first one and then the other taking the lead.

Behavior after disturbances.—Although moose at times may leave the impression that they are not very alert, because they can be approached closely without visible alarm reactions, this is not actually true. Their senses of smell and hearing seem particularly well

developed. As with some other mammals the position of the ears seems to be a good indicator of the level of alertness. When alerted, the ears are extended upward at a 45° angle to the head (Plate I).

The flight or flushing distance of moose seems to vary somewhat. Occasionally they can be approached to within 100 feet without causing undue alarm. Often moose will not show any sign of alarm when they are initially disturbed. Frequently they will raise their heads and stand quietly for about one minute or more. Then they will slowly move to the shore, where they will generally stop and look back. Often they shake their body or head to rid themselves of excessive water. Once covered by brush, they may continue to move in a slow pace, but often they will run, indicating more alarm than one might suspect.

Moose sometimes react quickly to non-human disturbances. For example, on one occasion in 1955 two bulls were observed to be alarmed by low-flying mergansers and rapidly moved into the bush. We do not consider that the approach of observers prealerted these animals.

The influence of weather on movements of moose.—Since psychic factors may interact with weather factors to exert an influence on the movements of moose, it is not an easy task to determine the effect of weather factors alone on these mammals. Moreover, various weather factors, such as temperature, wind, barometric pressure, vapor pressure and precipitation often have a combined influence, so it is difficult to assess the effect of one of these factors alone. Thus obvious relationships between moose movements and any single factor cannot be readily indicated.

Darling (1937) is one of the first workers to analyze in a rather detailed fashion the influence of weather on the movements of a big game species (red deer, *Cervus elaphus*). He found that these deer are often much affected by great variations in temperature, and that their movements are toward steadier temperature conditions. He did not discern any influence of barometric pressure on their movements. According to him, the state of wetness or dryness of the atmosphere was one of the most potent influences on movement: high atmospheric humidity tended to restrict day-to-day movements and a dry atmosphere induced it. Humidity obviously conditions other weather factors, e.g., damp atmosphere blankets the effects of the sun, and dry clear conditions allow for greater variations in temperature between day and night, sunshine and shadow. Darling found that red deer tend to move upwind. While steady rain tends to restrict movement, rain *per se* does not appear to exercise much influence.

Skuncke (1949) mentions that moose in Sweden are greatly affected in their habits by certain weather conditions. In windy weather, when a moose has difficulty in hearing or in picking up scent, it will lie up in dense forest cover. In fog and rain it also retires. In warm, clear weather the moose rests in the morning.

An effort was made in this study to measure the combined or separate effects of temperature and humidity on the movements of moose. It is realized, of course, that relative humidity is to some extent covariant with the temperature. Daily observations were plotted against maximum daily temperatures and relative humidity. It was believed that maximum temperatures influence moose movements to a greater extent than average daily temperatures, as moose seemed to be observed more on hot afternoons. Afternoon moose observations were plotted since these are liable to be affected more by maximum temperatures than morning observations. No obvious combined effect of these two weather factors on moose activity could be demonstrated. About 90 per cent of the observations fall in the following range limits: maximum temperature, 68 to 90°F.; relative humidity, 35 to 80 per cent. These are, however, roughly the limits for most maximum temperature–relative humidity conditions during the period May 1 to August 31.

No correlation could be demonstrated between daily temperatures, or temperature fluctuations throughout the summer, and the number of moose observations. Analysis of the data indicated that there is no recognizable difference in numbers of observations on warm or cool days.

In order to eliminate extraneous variables as much as possible, the observations made in

1955 on a definite route traveled in one direction only during the same time of the day (approximately 5:00 to 9:30 PM) were also examined for any correlation between moose observations, maximum temperature, and relative humidity. On 20 different trips between June 9 and August 27, from one to thirteen moose were observed per trip. The time period per moose observation ranged from 19 min. to 8 hr. 45 min. Temperatures ranged from 68 to 92°F. and relative humidities from 37 to 95 per cent. No correlation could be established between moose observations and weather factors mentioned. For example, it was noticed that on July 28, when 13 moose were observed, there was a low relative humidity. However, on June 16, under similar weather conditions, only three moose were noticed.

The author was thus unable to find temperature-humidity relationships similar to those observed by Darling. It is realized that movements in the water are mainly governed by the urge to feed on aquatics, and that these movements may not be representative of the diurnal activity rhythm outside an aquatic environment.

The 1955 data were similarly analyzed for a possible correlation between wind velocity and observed movements. Wind data were not recorded in the field, but were obtained from the Chapleau Forest District weather reports, taken approximately 70 miles south of the study area.

An analysis of the data from June 3 to August 31 shows no significant relationship between the number of minutes required in the field per moose observation and the recorded wind velocity. With winds of more than 10 mph, 27 moose were observed in 3,173 min. of observation, or 118 min. per observation. With winds of less than 6 mph, 45 moose were seen in 5,385 min., or 120 min. per moose observed. These data do not indicate any noticeable difference in the effect of wind velocity on moose observations in an aquatic environment. Since it was not possible to go out on the lake on the windiest days, these observations may be somewhat biased. It is entirely possible that moose movements were more restricted on days with high winds.

Fog does not appear to greatly hinder the movements of moose in the water. During early fall, moose were repeatedly observed feeding in the early morning in heavy to light fog.

Rain, especially steady pouring rain, may affect the movements of moose in the water to some extent, although these animals are regularly observed feeding in the water during light to medium rain. Not much quantitative information could be collected about this weather factor, because during heavy downpours we were usually unable to make observations.

During the period June 3 to August 31, 1955, eight moose were observed during 1,430 min. of observation in actual (usually light) rain on nine different days, or one moose observation per 180 min. When this admittedly small sample was compared with the one taken on days with or without light winds, and with mostly clear skies, it was noticed that about 50 per cent more moose were observed under the latter conditions (120 min. per moose observed).

Daily activity of moose.—In order to obtain further information regarding the activity of moose in respect to the time of day, all moose observations were recorded with the time of observation as well as the total duration of observation periods.

Data which accumulated during the entire study period, as well as additional data obtained in the Sioux Lookout District by A. T. Cringan during the summer of 1954, were submitted to L. M. Morrison, Statistician of the Department of Lands and Forests, Ontario, for further analysis.

It appeared during the field work that moose were more readily observed during morning and evening hours than during the middle of the day. More time was, however, spent on observations during the midday period. In order to obtain larger samples for statistical analysis, the data were gathered into three time groups, namely 3–9 AM, 9 AM to 6 PM, and 6–12 PM E.S.T. (Table 1).

The procedure followed in the analysis was to treat years as replications, and use the

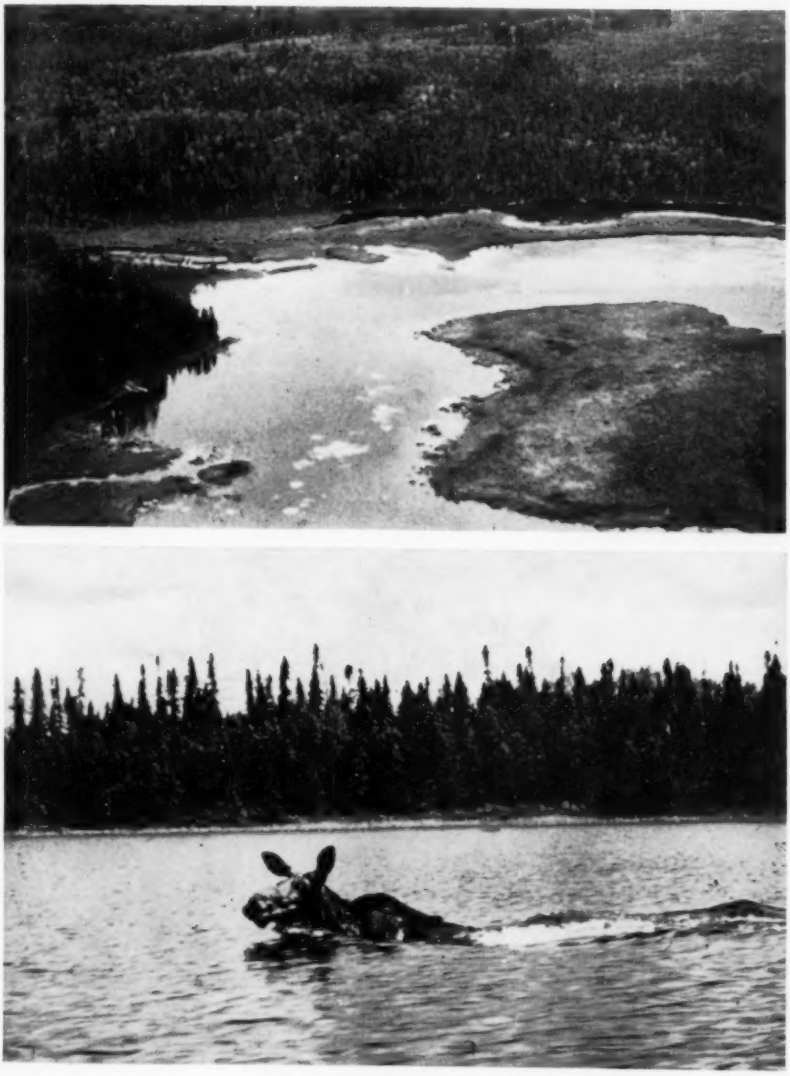

PLATE I

TOP: Aerial view of a shallow bay rich in aquatic vegetation. The bay is bordered by swales consisting of emergent aquatics.

BOTTOM: Adult cow moose with its ears in the "alert" position. In the background is mediocre aquatic vegetation. Photographs by Hugo Maliepaard.

PLATE II

TOP: A cow moose feeding on submerged aquatic vegetation.
BOTTOM: View of a shallow bay with considerable emergent vegetation.

interaction of years and times of day as an error term. If the anticipated difference in movement during the hours observed is real, it should show up similarly in each year, and over a number of years an average should become manifest which may be regarded as highly probable if there is not too much contradiction from year to year, which does not appear likely.

TABLE 1.—*Moose seen and hours of observation, versus time of day (E.S.T.)*

TIME OF DAY	1952		1953		1954		1955	
	Moose seen	Hours of observation	Moose seen	Hours of observation	Moose seen	Hours of observation	Moose seen	Hours of observation
3–9 AM	6	19	15	38	14	56	34	119
9 AM–6 PM	38	255	46	265	14	145	31	158
6–12 PM	22	37	10	96	1	25	107	166

As may be seen in Table 1, one of the serious weaknesses in the data is that far more hours were spent on observations during the middle of the day than either in the morning or at night. Observations before sunrise were often hampered by the presense of fog; after sunset a powerful flashlight was used to locate moose. Often, however, these animals managed to disappear into the forest before the light could be focussed on them, resulting in fewer observations. More time was obviously spent in the field during the middle of the day while traveling back and forth.

An analysis of variance and covariance did not provide a significant result. The data indicate that moose will be seen in the early and late hours more frequently than at the middle of the day but the evidence is not strong enough to establish the point at any accepted confidence level.

Adjustments made by covariance indicate that if the total of 1,379 hours spent in observation had been devoted equally to the morning, midday and evening periods, one might expect to see 146 moose from between 3–9 AM, 7 moose from 9 AM to 6 PM and 185 moose from 6 PM until midnight. This is, however, merely an indication based on the data in their present form. There must be some loss of accuracy when the sample is not taken exactly as it should have been.

It is not clear from our data whether moose activity continues to be high from midnight until 3 AM. It appears, however, that there are two peaks in activity, namely early in the morning (from approximately 6 to 9) and late at night (from approximately 5 to 10), with slightly greater activity during the latter period.

Further information about the activity pattern was obtained by recording with a simple stop-clock mechanism the time when moose were tripping paint traps set up to mark these animals (de Vos, 1956). The stop clocks provided the following records:

July 13, 1954	6:30 AM
July 15, 1954	7:30 AM
June 7, 1953	7:00 AM
July 13 and Aug. 8, 1954; Aug. 25, 1953	9:30 AM
May 30, 1953	5:15 PM
July 15, 1954	6:00 PM

Although these data are very limited, they appear to substantiate the activity pattern as already mentioned.

Figure 2 shows observations of adult moose, grouped by sexes, plotted against three-hourly periods of observation. The graph indicates that a higher bull-cow ratio was observed during the period 9 AM to 6 PM than during the periods 3 to 9 AM and 6 PM until midnight. No plausible explanation can be given for this apparent difference in activity between the two sexes. As moose censuses are usually made during the middle of the day, sex-ratio data may be accumulated which may not represent the exact picture.

Aquatic food habits.—The main reason why moose are so frequently observed in the water during the summer is, in my opinion, the availability of large quantities of aquatic vegetation and not an effort to rid themselves of flies and mosquitoes. It is not implied in this statement, however, that the behavior of moose is never affected by these bothersome insects.

The abundance and distribution of aquatic vegetation seems to govern the distribution of moose along lakes and streams. Figure 1 shows the correlation between moose occurrence and the abundance of aquatic vegetation. This figure is a modification of one in the author's paper of 1956, since additional data were collected in 1955. Moose are most commonly seen in Ontario during the summer where streams enter into lakes or in shallow bays (Plate I). Here there are usually shallow swales covered by semiaquatic vegetation (Plate II). Moose do not feed as much in the swales as along their edges, where there is the highest abundance of submerged or emergent aquatics.

No information can be presented at the present time about the importance of the role that aquatics play in the food habits of moose. It may be that a certain amount of aquatic food is essential to moose and that the relative availability of this source of food may constitute a limiting factor in the carrying capacity of a range. It should be noted that beavers, muskrats, ducks, and to some extent other big game species also utilize aquatics and therefore compete with moose for this resource.

Moose may, at times, feed continuously on aquatic vegetation in the same location for as long as several hours; at other times they may only feed for a few minutes. The "average" feeding period of an undisturbed moose seems to be about an hour. Where there is a good

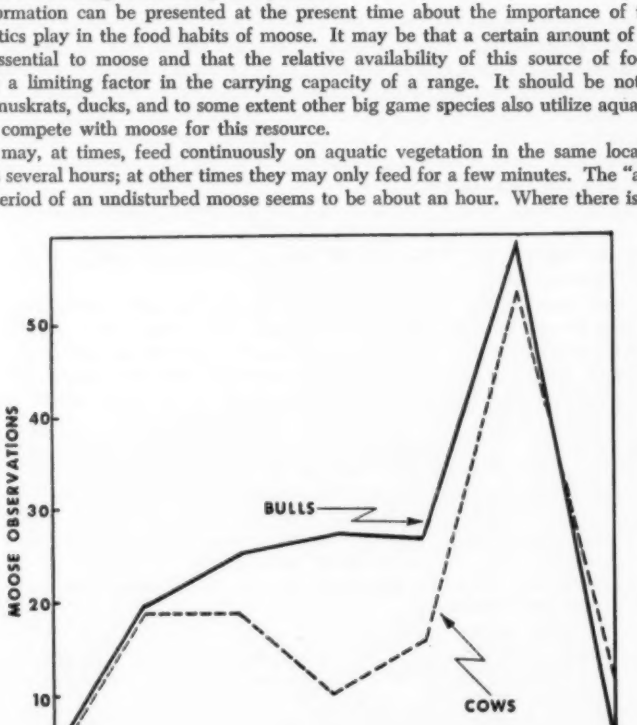

FIG. 2.—Moose observations plotted against three-hour periods of observation for both sexes indicate that a higher bull-cow ratio is observed at midday than early in the morning or in the evening.

supply of pondweed and eelgrass, individuals seem to linger on at one site, as illustrated by the following example: On August 13, 1955, a cow was first observed at 1:55 PM. She fed until 2:30 PM, when she went ashore, and lay down in the bright sun for about 45 minutes. She returned to the water to feed and was still there at 9:30 PM. The next morning she was seen feeding at the same place at 8:00 AM.

Moose feed normally by submerging the head to pull out aquatic vegetation. However, where the water is deep they have to dive for their food. In places where food is abundant, individuals may dive continuously for an hour or more. Normally the animals remain underwater for about 10 to 25 seconds, but occasionally they may submerge for 45 seconds.

Feeding on aquatics was observed at all times of the day. It often continues after sunset. Utilization of aquatic vegetation seems to be governed by availability and palatability. Such feeding starts relatively late in the year, because these plants require a period of development after the water begins to warm up. No feeding on aquatics was observed during the month of May, and the earliest record we have is for June 3, 1955. The peak of utilization is in late June, July and early August.

Aquatic plants are consumed continuously until late in October. Starting in late August, however, moose are seen in the water with less and less frequency. They are then seen usually on warm, sunny days. Peterson (1955) states that the decline in the amount of aquatic feeding seems to be correlated with a reduction in the palatability of the vegetation and that by this time most plants become tough and soured. In the opinion of the present author this may be somewhat overemphasized and possibly other reasons, such as rutting activity and depletion of the available supply, may be equally important.

Table 2 shows in chronological sequence the utilization of aquatic plants. The plants were either eaten or pulled out and left floating in our presence. A "?" in the table indicates uncertainty as to a plant's actual consumption by moose. Data are from the years 1953, 1955 and 1956.

In early June, horsetail (*Equisetum*) seems to be the only emergent plant eaten. Although horsetail was associated with a vitamin deficiency in domestic stock, this does not seem to affect the moose, possibly because insufficient quantities are utilized. After the middle of June little utilization of horsetail was noted, suggesting a possible decrease in palatability.

During June and July there seems to be a steady increase in the utilization of the following aquatics: eelgrass, *Vallisneria americana*; pondweed, *Potamogeton* spp.; yellow pond lily, *Nuphar advena*; and bulrush, *Scirpus* spp.

On Little Missinaibi Lake the following species of aquatics were present: *Myriophyllum heterophyllum, M. alternifolium, M. exalbescens, Sagittaria latifolia, S. rigida, Utricularia vulgaris, U. minor, Sparganium chlorocarpum, Chara* spp., *Potamogeton gramineus, P. Richardsonii, P. epihydrus, P. vaginatus, P. robbinsii, P. natans, P. amplifolius, P. pusillus, P. perfoliatus, Vallisneria americana, Scirpus* spp., *Zizania* spp., *Equisetum* spp., *Nuphar advena, Glyceria borealis,* and *Epilobium*? (a semiaquatic). No utilization could be ascertained of the genera *Myriophyllum, Utricularia* and *Sparganium,* possibly indicating low palatability to moose. Peterson (1955) reports utilization of the latter genus in Algonquin Park.

The leaves of the yellow water lily did not reach the surface until June 2, 1953, but were floating on June 1, 1955, an early year. On several occasions moose were noticed to eat the side roots and the growing tip of the rhizomes of this water lily, and also the petioles, flowers, and leaves. Beaver also use *Nuphar* but the rhizomes themselves are often chewed over their entire length. The rhizomes seem to be pulled up chiefly in June and early July occasionally in large quantities. On several occasions large numbers of water lily flowers were also seen to be eaten in places where moose were observed at other times.

Eelgrass is widely used during the period from July to September. It is available in large quantities and is the chief aquatic food in this area. Pondweed is another principal moose food which is very common in Little Missinaibi Lake. Several species are utilized.

TABLE 2.—*Chronology of utilization of aquatic plants*

DATE	AQUATIC VEGETATION EATEN OR PULLED OUT
June:	
3	*Equisetum*
3	Roots of rhizomes of *Nuphar advena*
5	Roots of rhizomes of *Nuphar advena*
9	Petioles of *Nuphar advena*
10	Roots of rhizomes of *Nuphar advena*
13	Many flowers of *Nuphar advena* clipped off?
26	Many stems of *Scirpus* clipped off at water line
27	Petioles of *Nuphar advena*
July:	
7	Great many rhizomes of *Nuphar advena* floating
8	*Vallisneria americana* in 5 feet of water
18	*Vallisneria americana* in 5 feet of water
19	Leaves of *Nuphar advena*
19	*Vallisneria*
20	Leaves of *Nuphar advena* and *Vallisneria*
21	*Sagittaria, Vallisneria, Glyceria borealis, Epilobium?*
22	Leaves of *Nuphar advena*
22	Leaves and flowers of *Nuphar*; many rhizomes pulled out. *Menyanthes trifolium*
25	*Vallisneria* in 2 feet of water
27	*Scirpus, Vallisneria*
28	*Vallisneria*
31	*Vallisneria* and *Scirpus?*
August:	
3	*Potamogeton epihydrus, Vallisneria*
5	*Vallisneria*
6	*Potamogeton**
6	*Equisetum*, roots and lower parts of stems
6	*Potamogeton, Vallisneria*
7	*Vallisneria, Potamogeton*
11	*Vallisneria, Potamogeton*
11	*Zizania*
17	Leaves of *Nuphar advena* eaten off tops of stems
23	*Potamogeton*
30	*Vallisneria*
	Perrault Falls area, Sioux Lookout, 1954 (courtesy A. T. Cringan):
July:	
13	*Potamogeton richardsonii*
27	*Carex rostrata?*
13	*Potamogeton natans*
13	*Sparganium, Vallisneria?*

* The following species, eaten by moose, were identified: *Potamogeton pusillus, P. natans, P. amplifolius, P. gramineus, P. perfoliatus.*

Moose often obtain this food by diving. Pondweed is most heavily used during August. Wild rice (*Zizania*) was present in only one arm of the lake, but there it seemed to be heavily used by moose.

It is interesting that we never noticed utilization of various species of *Carex*, which are widely available throughout the study area. This may indicate that these plants are less palatable to moose. Among the other semiaquatic plants we noticed grazing on buckbean (*Menyanthes trifolium*).

Bulrushes (*Scirpus*) are occasionally eaten throughout the summer but do not seem to be highly palatable. Utilization indicates that they are more palatable in the early summer.

Acknowledgments.—This study was financed by the Fish and Wildlife Division of the Department of Lands and Forests of Ontario. I am particularly indebted to C. H. D. Clarke who permitted me to conduct this work, first as a sideline to other activities, and subsequently as a project in 1955. I am also grateful to F. H. Montgomery for checking the identification of aquatic plants. E. I. Sillman was good enough to critically read the manuscript.

SUMMARY

Summer observations on moose behavior in an aquatic environment in Ontario during 1952, 1953 and 1955 are discussed. Moose are somewhat vocal during the summer. Three different calls can be recognized: an alarm call and two different communication calls between a cow and her offspring. Moose congregate in certain places because of a high availability of aquatic food. Feeding on aquatics starts in early June and terminates in late October. The peak of utilization is in late June, July and early August. Lists of aquatic vegetation are presented. Definite effects of temperature and humidity on the movements of moose could not be demonstrated. There was no apparent difference in moose activity on warm and cool days, nor at times of wind or rain. Field data indicate that moose will be seen less frequently at midday. The evening peak of activity seems to be slightly higher than the morning peak. During the middle of the day the ratio of bulls to cows was higher than in the early morning or during the evening.

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PARASITES AND DISEASES OF THE WELLS GRAY MOOSE HERD

By R. W. Ritcey and R. Y. Edwards

Studies begun in 1950 of the moose (*Alces americana*) herd in Wells Gray Park, British Columbia, have included a program of taking moose for autopsy. To date there are records of 34 such examinations. These, when augmented by incomplete data from approximately 100 moose harvested annually by hunters, have given some data on diseases and parasites associated with this herd.

The record is of special interest because the area inhabited by these moose appears to be one of the most productive ranges supporting moose in this

province. The result is that, with few exceptions, moose in this area have been in good condition the year round during the study period. Almost without exception cow moose taken in the hunting season are reported as fat, and comparable in this respect to medium fat beef. Bulls are not so fat, but are usually regarded as in good condition. Even in March or April, autopsied cows are usually recorded as with considerable deposits of fat on the omentum, and often with as much as ¾ to 1 inch of fat covering the kidneys. Kidney fat indices, as described by Riney (1955), were obtained from five moose in 1956. Here an index of 100, indicating that the weight of kidney fat is equal to the weight of kidney, probably indicates heavy reserves of fat. Two cows killed in January had indices of 256 and 159. A mature bull taken in late February had an index of 106. A cow killed in March had an index of 201, and another taken in April had an index of 121. It is worth noting that the winter of 1955–56 is considered to have been one of the severest as to temperature and snow depth since the beginning of the study.

Moose are numerous in the park. In summer the population is scattered through extensive subalpine forests. In winter there is concentration into old lowland burns rich in willow and birch browse where, locally, there may be up to 100 moose per square mile for extended periods of weeks. In 1952, aerial and ground censuses indicated a total population of 2000 on winter range (Edwards, 1952, 1954) with an average stand of about 30 per square mile over about 60 square miles of the winter range then in use. Since then, annual track counts of migrating moose account for about 1000 animals, which are known to constitute only part of the herd.

The country inhabited by this herd has a foothill topography penetrated by wide valleys with flat bottomlands. Mature lowland forest consists of cedar (*Thuja plicata*), hemlock (*Tsuga heterophylla*), spruce (*Picea engelmannii*) and balsam fir (*Abies lasiocarpa*). This is the forest of the northern portion of the Interior Wet Belt. Most lowlands in the park have been burned, however. Fire has created extensive stands of willow (*Salix* spp.), aspen (*Populus tremuloides*) and birches (*Betula papyrifera* and *B. glandulosa*). The fauna associated with this moose herd contains relatively good densities of mule deer (*Odocoileus hemionus*), caribou (*Rangifer arcticus*), goat (*Oreamnos americanus*), grizzly bear (*Ursus horribilis*), black bear (*Euarctos americana*), wolf (*Canis lupus*) and coyote (*Canis latrans*). There are also good populations of marten (*Martes americana*), fisher (*Martes pennanti*), lynx (*Lynx canadensis*), wolverine (*Gulo luscus*), mink (*Mustela vison*), beaver (*Castor canadensis*) and a host of lesser mammals. Cougar and bobcat (*Felis concolor* and *Lynx rufus*) are present but not numerous. The area is rich faunistically, a result of fertile soils and a diversity of habitats due to variations in successional stage and in elevation, and the influences of a diversified topography.

Most autopsies were performed in winter under the rough field conditions which must accompany most research in wild areas. It is entirely possible that, in performing examinations on such large animals in cold weather and

in deep snow, some diseases, parasites and abnormalities have been overlooked. There may be parasites and diseases in this herd yet to be recorded, and the incidences of infection of those conditions found may be higher than the data indicate.

We are indebted to the administrative personnel of Wells Gray Park, and to Messrs. Ted and Roy Helset, for their assistance in many winter autopsies; and to the many guides and hunters who co-operated in examining moose killed in hunting seasons.

PARASITES ENCOUNTERED

Moose tick, Dermacentor albipictus.—This tick is the only ectoparasite recorded from the herd. It is common, and can be easily found on most animals from about late February to May when the female ticks are engorged. The abundance of these ticks varies considerably among host moose, and the frequency with which heavy tick loads are encountered is quite variable from year to year.

Our experience with this tick is confined chiefly to the spring. Few ticks have been found during numerous autopsies from September to about mid-February, presumably because the gross methods of examination we must usually employ are not efficient enough to detect ticks of small size. Early in 1956 Ritcey endeavored to find ticks on several moose killed for autopsy. He found none, even after plucking hairs from large areas and using a dissecting microscope for close examination. By contrast, ticks are obvious on these moose from late February to May, engorged females seeming to appear coincident with the appearance through the snow of the first bare ground, and with the beginning of pelage molt in the hosts.

Ticks cause considerable irritation. In 1952, a year of heavy tick loads, moose were observed shaking their heads, scratching heads and ears with hind feet and even thrashing their heads in willow bushes.

On the snow of late spring, moose beds frequently contain live ticks as well as blood patches. The frequencies of occurrence of ticks in beds are shown in Table 1. These numbers represent ticks not eaten by birds, a variable loss which may render such counts inaccurate beyond indicating tick abundance in a general way. Robins, flickers, crows and "a small grey bird" (probably junco) have been observed to take ticks from moose beds.

TABLE 1.—*Annual occurrence of ticks observed in moose beds in snow, March and April*

YEAR	NO. BEDS EXAMINED	NO. TICKS SEEN	NO. TICKS PER BED
1953	66	95	1.4
1954	230	112	0.5
1955	157	21	0.1
1956	262	0	0.0

At this time of year, ticks and blood are not confined to beds. Both may be dropped by moose as they forage or migrate. Occasionally areas up to five feet square are spotted with blood, as if from moose shaking themselves. In 1953 R. G. Miller followed the trail of a bull moose for 300 yards through snow. In that distance the moose had dropped 240 engorged ticks, plus six flat ticks, the last probably males. The moose had lain in two beds, so the time interval during which ticks were lost was at least several hours.

There is annual variation in the abundance of ticks on these moose. In the springs of 1952 and 1953 tick loads were heavy. They were moderate in 1954, and light in 1955 and 1956. In years of heavy loads some extreme conditions have been recorded. Through late

March and early April in 1952 most moose beds were bloodstained and contained ticks. Thirty-one ticks were found in one bed. In that year a weak calf, reported by Patrolman C. E. Gaglardi, was captured and examined. It had ticks over most of the body with the exception of the back and shoulders. Forty to fifty engorged ticks were packed about the anus in an area about 4 inches in diameter. Similar patches, estimated at 60 ticks each, were located inguinally next the thighs. There was little space for more ticks on the ears, inside or out. The body was dotted with clusters averaging three or four ticks each.

It will be apparent that most of our data on ticks is obtained when snow is on the ground. Our experience may therefore be limited to the first part of the period when ticks are most active on moose. Not only is snow an aid to recording signs of tick occurrence and abundance, but with the disappearance of snow most moose migrate out of the area where it is possible to study them with some intensity. For this reason, our knowledge probably covers only part of the engorging period. This may account for our not being entirely sure that we are observing the life history of this tick as it is described in the literature. Hearle (1938) recorded that engorged females drop to the ground in spring. Seed ticks hatch and remain there until cold weather in autumn stimulates them to climb vegetation to contact passing hosts. These remain on the host through the winter. In Wells Gray Park most engorged females are dropped on the bottomlands of the valleys. Moose do not return to these bottoms until they are covered with snow in late autumn or early winter. Most moose must be reinfected, then, from seeds hatched from a relatively few female ticks that are carried to higher elevations in late spring.

There must be heavy annual mortality among these ticks. Engorged females begin to drop in numbers when patches of bare ground are beginning to show through the snow, but large numbers fall on snow where they are conspicuous and are fed upon heavily by birds of several species. Most females dropped are strewn across range which will not be inhabited again by appreciable numbers of moose until early winter. Unless the seed ticks produced by these females can remain active in cold weather and a foot of snow, the bulk of them have little chance of finding hosts on which to complete their life cycles. Perhaps here is yet another example of the heavy mortality which parasites can withstand, yet still flourish. Perhaps such losses are easily offset by a high reproduction potential, for Hearle (1938) recorded that females lay about 4000 eggs.

In our experience, heavily infested moose are not seriously weakened by ticks alone, although there is some evidence that moose weakened by other means, as by malnutrition or age, may carry particularly heavy tick loads which are an additional threat to the survival of the host. Presumably healthy moose are resistent to heavy loads of ticks, employing the same combative mechanisms used against any parasite entering its tissues.

Nose fly, Cephenemyia sp.—Larvae of this fly, probably *C. jellisoni*, have been found in only two moose autopsied. In both cases only one larva was found. By contrast, deer in many parts of British Columbia are heavily infested by this species (Cowan, 1951). The few mule deer autopsied in Wells Gray Park have yielded only one larva of this parasite.

Both records from moose were obtained in 1953, one from a mature cow containing a larva among the posterior nasals, one from a 22-month-old cow containing one larva in the esophagus. Both larvae may have moved upon the death of their hosts.

Bladderworm, Cysticercus tenuicollis.—This larval cestode has been found in most moose autopsied. Excluding two autopsied animals in which decomposition was too advanced to search effectively for these cysts, the bladderworm has been found in 84 per cent of the remaining 32 moose. The mean number of cysts per infected animal was 4.6; the mode was 2. We have found ten or more cysts in three moose, all of them with much worn teeth and probably over nine years old. Sixteen cysts were found in one of them.

Of 125 cysts found, loci were as follows: liver, 89; omentum, 25; heart, 7; one each for pancreas, mesentary near liver and mesentary near kidney. Some of these cysts were beginning to calcify. In addition, numerous well-calcified bodies have been found, mainly

in livers, which were suspected of being old cysts of this organism. One calf about nine months old had three of these cysts on its liver.

As noted by Cowan (1951) the presence of this parasite is the rule rather than the exception. Coyotes are common on this moose range, and wolves are present. These are probably the hosts of the adult form, the tapeworm *Taenia hydatigena*. We have never observed pathogenic symptoms to be associated with these cysts in moose.

Measles, Cysticercus sp.—Small, hard cysts, probably either *C. krabbei* or *C. ovis*, have been found in two animals autopsied, and have been reported from several of the hundreds of moose that have been taken by hunters. When present it is usually most common in the muscles of the thigh. There is one record of many of these cysts in the brisket, and one cyst has been found in a heart. Thigh infestations may be heavy, with cross sections consistently striking 1–6 cysts. Moose harboring the parasite have appeared healthy.

Hydatid cysts, Echinococcus granulosus.—This cyst has been found in 68 per cent of autopsied moose. The mean number of cysts per infected animal was 7.7: the mode was 1.0. Old animals tend to have the most cysts. Of 164 cysts found, 158 were located in lungs, five in liver and one in a kidney.

Two very heavily infected animals have been examined. One cow, 8 to 10 years old, had 32 cysts on the lungs. The animal appeared to be in good health, with heavy fat deposits about the kidneys. She was killed in late January. Her kidney fat index was 159.

Another cow, on March 6, 1955, was trapped in a large corral for tagging. As men approached the trap she advanced with defiant behavior, stopped, began to tremble violently, then sank slowly to the ground breathing heavily. Breathing became weaker, and the animal was dead in four minutes. Autopsy revealed she was about four years old. She had the heaviest hydatid infection that we have encountered. There were three hydatid cysts in the liver and at least 30 in the lungs, ranging from ¼ to 2 inches in diameter. The cow was pregnant with twin calves, had heavy fat deposits on the omentum, and fat ¾–1 inch thick over the kidneys. The only unusual feature found, aside from cysts, was an excessive amount of fluid in the pericardial sac.

The incidence of hydatid cysts is heavier on this moose range than in most game ranges studied by other workers. Rausch (1952) found conditions similar to those in Wells Gray Park and stated, "I would expect to find that nearly every aged moose in southern Alaska would harbor *Echinococcus* larvae." Green (1949) reported on large numbers of elk examined in Banff National Park. From 1.7 to 6.8 per cent were infected in different years. Cowan (1948) found it in one of many coast deer he examined and (1951) recorded it from one mule deer in Jasper National Park. Fenstermacher (1934) found hydatid cysts in 8 of 19 moose examined in Minnesota. Miller (1953) quoted Hatter's estimate that 50 per cent of the moose in British Columbia carry these cysts, while Sweatman (1952) found 59 per cent of 29 moose in Ontario infected. Peterson (1955) calls *Echinococcus* the most common parasite found in Ontario moose. Harper *et al.* (1955) studied hydatid infections in Saskatchewan. They found 30 per cent of 96 moose infected. They suspect that the incidence of infection in moose may be higher than their data suggests, since most material examined was submitted by hunters.

We have no data suggesting that heavy loads of these cysts have much influence upon either the physical condition or life span of hosts, except possibly for the case of the animal which "died of fright" as described above. Rausch (1952) reported, "The larvae of *E. granulosus* appear to be essentially non-pathogenic in their natural mammal host."

Parts of this moose range are heavily hunted in autumn, and part is inhabited sparingly by people on small farms. The abundance of this parasitic organism constitutes some danger to humans in the area. Canids are probably the main alternate hosts. Coyotes are fairly common throughout the range. Wolves, on the other hand, confine most of their activities to areas remote from the heavily hunted and farmed areas. Domestic dogs probably constitute the most serious danger in transmitting this organism to humans.

Work in Ontario has shown that fisher, *Martes pennanti*, can carry the adult tapeworm (Sweatman, 1952). It is possible, then, that mustelids generally may be potential hosts. The moose range in question contains populations of wolverine, otter, marten, fisher, mink and two weasels, all of which are suspect as hosts of adult worms.

The abundance of *Echinococcus* in Wells Gray Park is probably not unique in central British Columbia. Hatter's statement, given above (*vide* Miller, 1953), is based on experience throughout a large part of the province.

In this park, any control measure based upon control of the abundance of hosts of adult worms would be unrealistic. The expense involved in applying such controls to wild canids alone would be prohibitive relative to the benefits to be expected. In addition, the size of the area involved and the variety and number of predators in it preclude much hope of success in any event. If mustelids are hosts, any program directed at reducing their numbers would seriously affect the livelihood of trappers deriving a large part of their annual income from these mammals. Practicable control measures should be aimed at education of people as to the dangers of hydatid disease and how to avoid infection.

It has been suggested that control measures to reduce the abundance of this parasite would be accomplished by reducing the wolf population. There is no evidence to suggest that such control would assure fewer *Echinococcus* organisms, and in the final analysis there are many people who would rather have "wolf country" than an area where the slight chance of getting hydatid disease is made only a little slighter.

Legworm, Wehrdickmansia cervipedis.—We have failed to find this subcutaneous parasite in only two adult moose, and in three calves all 9 months old or younger. Of 27 moose examined for this organism and over one year old, 95 per cent were infected.

Most common sites of infection are on the feet and the brisket. In several cases, when especially numerous, large numbers have been found on the shoulders and sides. One case of three worms per square inch over part of the brisket has been noted. In no case have we noted inflammation to be associated with sites inhabited by this nematode.

OTHER CONDITIONS

Actinomycosis.—Actinomycotic-like lesions of jaw bones, particularly about the teeth, are frequently encountered in these moose. The most severe cases are found in old animals with worn teeth. Impacted food, fibrous in nature, is usually associated with this disease in severe cases.

Two examples of severe infections in old animals are given below. In May, 1950, P. W. Martin examined an aged cow that was very thin. Severe necrosis was found between two molars in bone, gums and cheek tissue. Both molars were loose. The cheek lesion perforated the cheek, forming a hole an inch wide. Food had been passing through this hole from the mouth. The necrotic area between the teeth was impacted with a large amount of fibrous vegetable matter.

In 1952 an old cow died in early winter. Her remains were examined the following spring. There was severe bone necrosis about the upper teeth. Two teeth had fallen from decayed sockets, and a third was hanging by one root. Quantities of tightly packed fibrous material were packed into necrotic cavities.

We have found this condition in five autopsied animals, and it is observed regularly in animals taken by hunters. This disease seems to be confined mainly to aging animals with worn teeth.

Contagious warts.—Warts have been encountered on only two animals autopsied. Infected animals have been seen in the field, and hunters report these growths occasionally. A severe case has yet to be noted. From February 2, 1955 to January 30, 1956, 51 moose trapped were negative for these warts.

Other diseases, injuries and abnormalities.—Symptoms of bacterial, fungus or virus disease have been encountered occasionally. There has been little opportunity to identify causative organisms. Several cases of swollen legs and feet, sometimes with lesions visible, are on

record. One liver examined had seven rice-like bodies resembling those of *Sarcocystis*, and another liver had extensive healed lesions, presumably from bacterial infection. There is one record of numerous kidney stones. Skin lesions, probably from mechanical injury, and scar tissue from such wounds that have healed, are frequent. Healed rib fractures are common. Healed fractures of the leg have been noted. Four blind eyes and one with a foreign object embedded in it have been examined. One case of twins, each blind in one eye, suggest an inherited deformity. Also on record are a deformed hoof (elongated), a branching renal artery entering the kidney in two places and several cases of supernumerary teeth.

Careful search in most animals autopsied has failed to reveal nematode lungworms.

SUMMARY

A moose herd in British Columbia, which appears to be inhabiting exceptionally good range, harbors the following organisms in some abundance: moose tick, bladderworm, hydatid cyst and legworm. Also present are nose fly, measles, contagious warts and actinomycosis. Bladderworm, hydatid cyst and legworm were found in 84, 68 and 95 per cent, respectively, of the moose examined.

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GENERAL NOTES

EARLY FUR RETURNS FROM THE PACIFIC NORTHWEST

Long before governmental wildlife agencies existed in the Pacific Northwest, the British Hudson's Bay Company, through monthly and annual fur reports from its far-flung trading posts, provided a source of information on relative populations of economic mammal species. Although most of the historic fur statistics relate to Canadian areas, there were a few H.B.C. outposts in what is now the state of Washington for which fur records are available. One of these was Fort Nisqually, established in 1833 as the first trading post on Puget Sound. Situated about 17 miles south of present-day Tacoma, it became a center of trade with the Indians and between the English and Americans during its 37-year existence. The Fort Nisqually Journal for 1833–36 (Vols. 1 and 2, Hunt. MSS FN 1234) and Fort Nisqually fur trade reports for 1843–70 (Hunt. MSS FN 1245) are in the manuscript collection of the Henry E. Huntington Library of San Marino, California, and the author is indebted to that library for permission to excerpt pertinent details on this fur enterprise. The research was made possible by a grant from the Fund for the Advancement of Education to investigate American frontier wildlife conditions.

Although no specific locality records are available, the pelts received at Fort Nisqually were probably trapped in southern British Columbia as well as in Washington, largely by Indians. In Table 1 there is a compilation of the reported returns for ten selected years, the species listed in decreasing order of abundance. All of the species except the sea otter

TABLE 1.—*Compilation of annual fur returns, Fort Nisqually (Washington), 1834-1870*

SPECIES	1834	1835	1843	1846	1849	1850	1851	1858	'05–65 (1 yr.)	'69–70 (1 yr.)	Total	Rank 1946*
1. Beaver	1450	1454	430	330	149	88	163	169	429	458	5120	
2. Muskrat	700	801	287	667	418	149	312	13	1	106	3454	1
3. Raccoon	190	515	234	192	219	180	283	28	12	132	1985	5
4. Otter, river	340	377	162	154	110	110	174	52	31	74	1584	9
5. Bear, black, brown	46	37	35	81	78	72	83	20	12	69	533	
6. Mink	80	54	54	47	22	28	46	1	6	73	411	2
7. Lynx	—	8	10	38	10	30	44	13	—	—	153	
8. Fisher	9	28	16	17	7	15	27	3	—	11	133	
9. Otter, sea	1	—	1	1	—	1	—	—	31	4	39	
10. Marten, pine	—	7	2	9	5	—	2	—	—	4	29	7
11. Wolf	—	—	8	11	1	—	1	2	—	—	23	
12. Bobcat	—	—	—	—	—	—	—	—	—	21	21	8
13. Seal, fur	—	1	—	—	—	—	—	—	—	15	16	
14. Fox, red	—	—	1	1	3	8	—	2	—	—	15	10
15. Wolverine	—	10	—	—	—	—	1	—	—	—	11	
16. Skunk	—	—	—	—	—	—	—	—	—	2	2	4
17. Lion, mountain	—	—	—	—	—	—	—	2	—	—	2	
18. Badger	—	—	1	—	—	—	—	—	—	—	1	12

* Frank G. Ashbrook. 1948. Annual fur catch of the United States. U.S. Fish and Wildlife Service, Wildlife Leaflet No. 315: 23.

still exist in the state of Washington but, as indicated in the right-hand column, there have been some not surprising changes in rank in the past century, reflecting trends both in mammal populations and in fur styles.

At the beginning of this period, beaver and otter pelts were the standard. The big decrease in beaver returns between 1835 and 1843 is indicative of the cosmopolitan decline associated with the shift from the beaver-skin to the silk hat about 1839. The low return on wolverines suggests that these solitary mustelids were probably not even commonly encountered in frontier days, and the same may also have been true for fishers. The sea otter population had been depleted by Russian hunters and others by 1843 but exhibited some gain three decades later, only to be decimated again after the 1867 Treaty of Sitka which abolished controls.

Not included in the table for 1834 are two elk hides and 40 "Chev." The latter, also designated as "cheveran," "chevx" and "chiveraux," was derived from the French "chevreuil" or roebuck and must have referred to the black-tailed deer. In 1835 there were 220 more "chev." reported, eight "red deer skins" (probably the white-tailed), and 885 "wood rat" pelts. Why 1835 should have been a woodrat year is an amusing consideration, and what eventually happened to the pelts is even more intriguing. The first bunch of 20 was brought to the fort in March.

The Hudson's Bay Company, like other business-minded fur companies, preferred to pay for pelts in trade items. In 1843 a prime lynx pelt traded for one blue cotton handkerchief, a mink for 4 inches of twist tobacco, a fisher and large wolf for "six ball and powder" each, 18 raccoons for 4½ feet of twist tobacco and 10 ball and powder, 32 large beaver for two beaver traps and 30 plain blankets, and 32 muskrats ("muskquash") for 9 feet of tobacco, 4 ball and powder, and two small cod hooks. At the Fort Vancouver Indian Shop in 1842, one large beaver pelt (or two large otter pelts) brought any of the following: one plain blanket, one pair "corduroy trowsers," on broad scarlet belt, one yard blue duffle, one black silk handerchief, one cloth vest. The Company's preference for trade rather than cash transactions is readily appreciated when one notes that a large beaver pelt traded for a black silk handerchief which wholesaled in the Northwest at only about 55 cents. In 1869 Fort Nisqually was paying cash for its furs: large black bear pelts, $6; beaver, $1 a pound; gray lynx furs at $1; fisher pelts, $4–5; prime mink, 75c–$1; sea otter, $30; land otter, $4–5; and muskrats, 6¼c apiece.

During the earlier days of Fort Nisqually these furs were packed up, in the case of beaver in bales of 125 large pelts, and shipped to London by the Company's several ships. Into the respective fort's record books would go a notation on the month's returns; and these historic notations today afford some insight into bygone wildlife conditions in frontier North America.—Richard G. Beidleman, *Dept. of Biology, Univ. of Colorado, Boulder.* *Received February 18, 1957.*

NOTES ON MAMMALS FROM EASTERN NEBRASKA

The distribution of mammals in eastern Nebraska is poorly documented in the literature. In the past several years I have obtained reliable reports or seen specimens of several mammalian species from along the Missouri River, some of which help clarify the distribution of the species concerned in the eastern part of the state.

Lasiurus cinereus cinereus (Beauvois).—On June 16, 1956, I found an adult female hoary bat, now in my personal collection, on the sidewalk in Omaha, Douglas County, Nebraska. This animal contained two embryos.

Mustela rixosa campestris Jackson—I know of but one specimen of the least weasel taken in Douglas County. In January 1935, a least weasel (sex not recorded) in white pelage was collected on the Joseph Steyskal farm near Ralston, Nebraska. This animal was found

trapped in a large open-end barrel. Water was poured into the barrel to kill the animal which I later mounted.

Urocyon cinereoargenteus (Schreber).—The only record in the literature, known to me, of a gray fox from Nebraska is from Pierce, Pierce County (Swenk, Proc. Nebr. Acad. Sci., 8:123, 1908). On February 10, 1953, a gray fox was captured in the basement of the First Presbyterian Church, Omaha. The fox had seemingly gained entrance through a basement window after falling into an areaway. The animal was presented to the Riverview Park Zoo in Omaha but died after a short time in captivity. Gray foxes in eastern Nebraska are presumably referable to *U. c. ocythous.*

Lynx rufus (Schreber).—Bobcats formerly occurred in suitable habitat throughout Nebraska. Their distribution in the state at present is seemingly limited to more heavily wooded areas from the Platte River Valley northward. I know of no previous records along the Missouri River in the eastern part of the State. James Lombardo of Ft. Calhoun, Nebraska, reports to me (*in litt.*, March 26, 1956) that on July 31, 1955, he hit and killed a bobcat with his car at approximately 11:30 PM on U.S. Highway 73, halfway between Omaha and Ft. Calhoun, in Washington County. This animal, a young male weighing 22 lbs, was mounted and is now on display in Lombardo's Cafe in Ft. Calhoun.

Rudy Fick of Blair, Nebraska, reports to me that a bobcat was killed by hunters along the Missouri River bluffs, south of Blair, Washington County, Nebraska, on January 1, 1947. I have not been able to ascertain the subsequent disposition of this animal. Bobcats in eastern Nebraska are probably referable to the subspecies *L. r. rufus.*

Sciurus carolinensis carolinensis Gmelin.—There are only three localities of record for the gray squirrel in eastern Nebraska (Jones, Univ. Kans. Publ., Mus. Nat. Hist., 7: 482, 1954). Carl Schmidtmann of Omaha has in his possession a mounted gray squirrel, a male, that was obtained in October, 1924, on the William Wheeler farm near Rock Bluff, Cass County, Nebraska.

Sylvilagus floridanus mearnsi (J. A. Allen).—Since the first report of a melanistic Mearn's cottontail in Nebraska (Velich, Jour. Mamm., 37: 271, 1956), a number of additional records have come to my attention. Lawrence Tietz, who obtained one of the rabbits originally reported, obtained for me a second melanistic specimen that was shot by him on January 21, 1956, at the DeSoto Bend of the Missouri River, in Washington County, Nebraska. This rabbit is now in my personal collection. It is the fifth black cottontail that Tietz has obtained from the DeSoto Bend area. Three Omaha hunters are known to me to have shot melanistic animals in the above area in the 1955–56 hunting season. Rudy Fick brought me a black male cottontail that he shot in the DeSoto area on December 19, 1956. Unlike the specimens earlier recorded, all the animals I have recently examined have been entirely black; the pads of the feet vary in color from near normal to a sooty gray.

Apparently a population of *S. f. mearnsi* containing many melanistic individuals has become established in the area of the DeSoto Bend of the Missouri River. This population has been subjected to heavy hunting pressure owing to the desire among hunters of this area to obtain black rabbits. It is encouraging to report that plans are now being formulated by the Nebraska Game, Forestation and Parks Commission and by the Federal Fish and Wildlife Service to create a wildlife refuge in the DeSoto Bend.

A. E. Masilko of Omaha reports to me that he shot a melanistic cottontail in January, 1946, approximately 7 mi. SW Auburn, Nemaha County, Nebraska. Ray Moline of Omaha found a dead melanistic cottontail in the summer of 1955 that had been killed by an auto in Elmwood Park, Douglas County, Nebraska.—RALPH VELICH, *5212 South 23rd Street, Omaha, Nebraska.* *Received February 27, 1957.*

LOCALIZED VARIATION IN MASKED SHREW ABUNDANCE

Incidental to an investigation of factors affecting the regeneration of northern white cedar, *Thuja occidentalis*, following lumbering, the writer observed what appears to be an unusual instance of local extremes in abundance of masked shrews, *Sorex cinereus*, near Shingleton, Michigan. Since little is known concerning the ecology and population dynamics of soricids, the observations reported here may be noteworthy.

Primarily, the study was designed to provide information on species composition and comparative densities of small mammals on two forest plots, the Star Siding and Petrel Grade cedar-cutting projects. A total of 58 Museum Special snap traps were distributed in systematic grid pattern in each area. Due to differences of size and configuration between the cutting plots, traps were located at intervals of 66 × 132 feet at Star Siding and twice this spacing at Petrel Grade. Trapping began on August 15, 1955, and continued for four and five days on each area.

Only a few rodents were obtained from this trapping program. Common to both areas were the following: *Peromyscus maniculatus, Eutamias minimus, Tamiasciurus hudsonicus, Lepus americanus*, and *Erethizon dorsatum*. However, *Chethrionomys gapperi* and *Zapus hudsonius* were taken only at Petrel Grade.

It was surprising to find that although 25 masked shrews were captured in the Star Siding area, none were obtained at Petrel Grade. The high number of sprung traps, often containing tail segments, indicated that many more were present but escaped capture. Based on these results, a population density of approximately 4.2 shrews per acre was estimated for the 6-acre Star Siding area.

The situation described is perplexing in view of the essentially similar nature of the environments, although the areas are approximately 3 miles apart. Soils for each site consist of slightly alkaline Carbondale muck in which the water table is at or near the surface, even in midsummer. In addition to white cedar, the forests contain balsam fir, black spruce and tamarack. Swamp hardwoods are present in both areas, although more prevalent at Petrel Grade. It was suspected that microhabitat differences not readily recognizable, existed between the sites. Subsequent study of understory vegetation substantiated this observation to a degree. A scanty understory, comprised largely of tag alder, Labrador tea, shrubby cinquefoil and sphagnum moss, occurs at Star Siding. Ground vegetation typical of bog situations is occasionally encountered. Relatively few white-tailed deer use this area as a wintering yard, although snowshoe hares are generally abundant.

Site quality at Petrel Grade is apparently conducive to the establishment of numerous other deciduous shrub species, such as willow, red-osier dogwood and mountain maple. A mature stand of northern hardwoods is contiguous with one border of this area, thereby promoting the establishment of hardwood seedlings following opening of the stand through logging. The interspersion of deciduous plants in this area may be attractive to deer, since high numbers of deer overwinter here.

Despite the vegetational differences noted, their relationship to shrew abundance remains undetermined. Although considerable variation in size, conformation and cutting specifications of blocks occurs between projects, their net effect is probably slight. Cuttings were designed to range from extreme clear-cut to light selective harvests. While rank growths of vegetation, largely red raspberry and goldenrod, volunteered on the clear-cut blocks, little change occurred in other sites. Most shrew specimens were taken in uncut or lightly harvested timber while relatively few were taken in open, drier situations.

Insects, particularly ants, appeared to be plentiful in both aeras and were generally attracted to the peanut butter bait. The concentration of insects may have caused the shrews to investigate the traps.

Moisture, an important factor in distribution of this species, was not believed to differ between areas to any great extent. Moss-covered, rotting debris was everywhere abundant.

It may be significant, however, that the 1955 summer was unusually warm and dry. This may have caused local concentrations of shrew populations in the moister sites. Bole (Sci. Publ., Cleveland Mus. Nat. Hist., 5 (4): 15–77, 1939) observed the species at a peak in Ohio in 1937, with populations ranging from 1 to 11, although normally less than 1 per acre.

Although the determination of population density in this study is subject to criticism because of limitations in the method of sampling, the value obtained does not seem excessive for northern Michigan. Manville (Misc. Publ. Mus. Zool. Univ. Mich., 73: 1–83, 1949) found masked shrew densities of 4.12 and 3.09 per acre in northern white cedar and black spruce stands, respectively.

From limited information available it appears that shrew populations may not only be cyclic, or at least fluctuate widely from year to year, but also vary in abundance in areas of essentially similar environments, due to the influence of microhabitat differences. Minor changes in sites are often subtle and difficult to determine, except by detailed cover analysis.—Louis J. Verme, *Michigan Dept. of Conserv., Shingleton. Received October 19, 1956.*

MYOTIS KEENII SEPTENTRIONALIS IN SOUTH DAKOTA

The only record of *Myotis keenii septentrionalis* Trouessart from South Dakota known to us is an alcoholic specimen reported by Miller and Allen (Bull. U.S. Nat. Mus., 144: 107, 1928) from Elk Mountain, Custer County, one of the most westerly localities of record for the subspecies. Nevertheless, Elk Mountain seems to be within the normal geographic range of the species since the collection of the Nebraska State Museum contains two skins only of *M. k. septentrionalis* collected on June 7, 1900, also at Elk Mountain, by Merritt Cary.

The only other South Dakotan bat in the Nebraska collection is a specimen of *Corynorhinus townsendii pallescens* Miller from Hell's Canyon, 13 mi. W Custer, Custer County.

We are indebted to Dr. C. Bertrand Schultz and Mrs. Mary L. Pritchard of the above-mentioned museum for permission to report these specimens.—J. Knox Jones, Jr. and Robert L. Packard, *Museum of Natural History, Univ. of Kansas, Lawrence. Received January 21, 1957.*

NOTES ON A COLONY OF *BRACHYPHYLLA CAVERNARUM*

A colony of this large bat at Estate Sion Hill, St. Croix, U.S. Virgin Islands, was killed by gassing with a motor exhaust on December 13, 1956. Six wheelbarrow loads of the bats were raked up and removed from a dark chamber in the ruins of the old sugar factory. The first load was counted, sexed and found to consist of 276 females and 63 males (100 : 22.83), for a total of 330. There were thus approximately 2000 bats in the colony. The rest were examined with less care, but it was apparent that the unbalanced sex ratio was about the same throughout the collection. No other species of bat was present in the colony, although two mice (*Mus musculus*) were found gassed.

A few fleas were seen on the bats, but none was captured. Many individuals were infected with one or a few batflies (Streblidae).

The bats were all either adult or subadult. Twenty-five females were opened; none showed enlarged uterus, enlarged ovarian follicles nor grossly apparent corpora lutea. The males seemed more advanced sexually, with externally prominent testes mostly 4 to 6 mm. long.

These bats were killed by the estate owner in the generally shared belief that they were *Artibeus jamaicensis*, which does much damage to fruits in this locality. We know of no food habits studies on *Brachyphylla*, and have not adequate facilities to make one here.

However, an examination with a hand lens of the washed guano shows it to contain a high proportion of insect fragments, and some amorphous material which may or may not be fruit pulp. Seeds and partly eaten fruits of mango, East Indian almond, hogplum and other easily recognized species are abundant in *Artibeus guano*. No such material was found in the guano of *Brachyphylla*, although a few small seeds of what appears to be a species of *Eugenia* were seen. These seeds could have passed through the bats or been brought in by the mice. These observations could mean either that *Brachyphylla* is entirely insectivorous, or that it eats fruit but avoids small seeds, and cannot carry larger-seeded fruits back to the roost as does *Artibeus*.

The estate owner, Mr. Keith Merrill, who generously made the specimens available to us, told us that he had gassed the same room approximately a year ago and had removed seven and a half wheelbarrow loads of bats, or roughly 2500. The bats have evidently occupied this room for a great many years.—R. M. Bond and G. A. Seaman, *Kingshill, St. Croix, U.S. Virgin Islands. Received January 28, 1957.*

NEW RECORD OF CALIFORNIA GRIZZLY BEAR

On May 31, 1956 the partial skeletal remains of a California grizzly, *Ursus arctos californicus* Merriam, were found in the Santa Monica mountains approximately 3.5 mi NNE of Malibu Beach in Los Angeles County, California. The discovery site was the bed of an intermittent stream on the chaparral-covered northwest slope of Saddle Peak at an elevation of 1700 feet. This area lies specifically within the north central portion of Sec. 16, T. 1 S, R. 17 W (USGS 7.5 minute series, Malibu Beach Quadrangle, 1950). The bones recovered were partially buried in humus and silt, and show evidence of weathering, particularly on the left side of the skull. The animal had been lying on its right side, which yielded most of the material found.

The skeletal portions recovered comprise the following: skull, right mandible, right scapula, left ulna and a thoracico-lumbar segment from the right side. The latter includes the last seven thoracic vertebrae, the first two lumbar vertebrae, and ribs IV–X inclusive; these were in their natural articulated position and were lifted intact in a plaster of paris cast. The skull and right mandible are shown in Plate I.

The skeletal measurements of the specimen, in mm., are as follows: (1) Cranial measurements—*Condylo-basilar length* (occipital condyles weathered, their projecting surfaces estimated), 300; *breadth of rostrum*, just posterior to roots of canines, 72; *greatest length of nasals* (anterior borders somewhat weathered), 90; *breadth across post-orbital processes* of frontals, 96; *zygomatic breadth* (left zygomatic process missing, measurement taken from right zygoma to sagittal suture and doubled), 172; *mastoid breadth* (left mastoid process weathered, its projected surface estimated), 130; *alveolar length of tooth row*, anterior border of canine to posterior border of M2, 120; *crown length of P4 M1 M2*, 77; *crown length of M1 M2*, 52.8; *crown length of M2 alone*, 39.1; (2) Mandibular measurements—*Greatest length* (symphysis to posterior border of condyle, 221; *alveolar length of tooth row*, as above, 135.5; *crown length P4 M1 M2 M3*, 88.3; *crown length M1 M2 M3*, 75.7; *Crown length M2 M3*, 50.2; *crown length M3 alone*, 24.8; (3) Left ulna—*Length*, olecranon process to distal epiphyseal juncture, 285; (4) Right scapula—*Length*, acromion process along spine to dorso-posterior angle, 220.

The sulcate heel of P_4 can be seen in Plate I. An anomaly in dentition can also be noted in the supernumerary, upper left incisor socket. Tooth wear and skeletal measurements suggest that the specimen may possibly have been a relatively small female, aged 4–7 years. The evidence, however, is inconclusive, and such an appraisal, particularly as to sex and age, may be in error.

This specimen is the first collected in this part of the state (T. I. Storer, correspondence with A. L. Haines, Nov. 2, 1956). The nearest collection site of record is at the head of

Big Tujunga Canyon in the San Gabriel mountains where a grizzly was killed in 1894 (Grinnell, Dixon and Linsdale, FUR BEARING MAMMALS OF CALIFORNIA, I: 65–93, 1937).

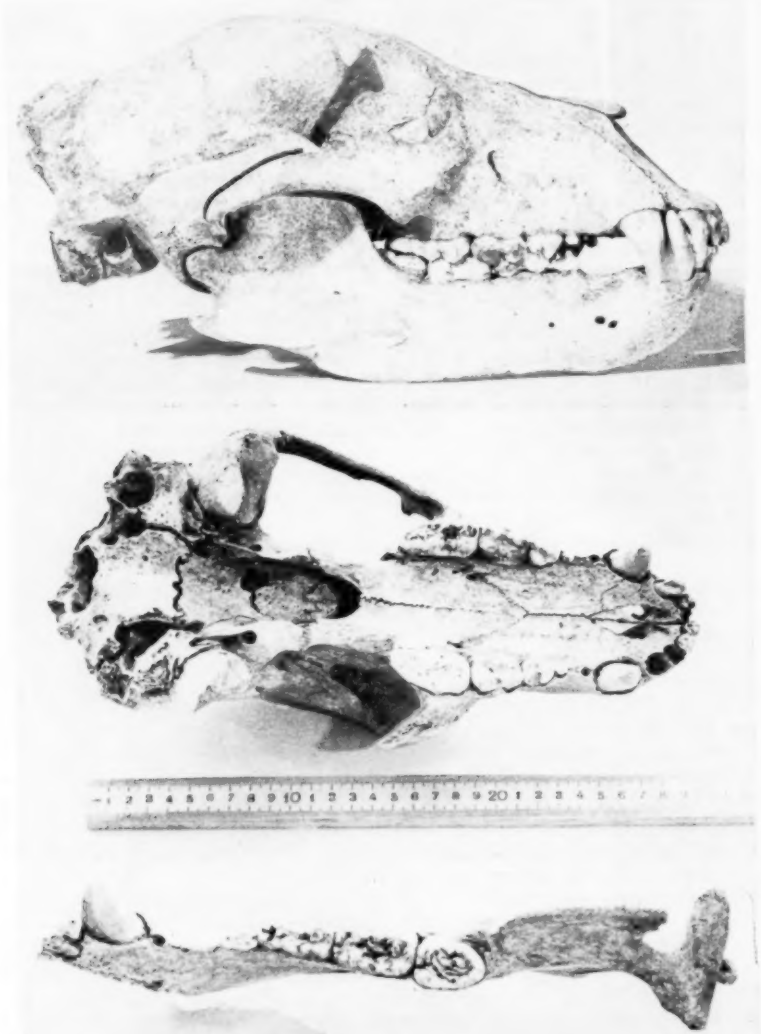

PLATE I

TOP: Skull and right mandible in full occlusion, lateral view; CENTER: skull, occlusal view; BOTTOM: right mandible, occlusal view.

In 1916 a bear was trapped in this same canyon but its identification as that of a California grizzly is subject to considerable question (Storer and Tevis, CALIFORNIA GRIZZLY: 287–288, 1955). The record here reported would indicate that the California grizzly not only ranged through the Los Angeles plain, San Gabriel and Sierra Madre mountains (Grinnell *et al.*), but in the Santa Monica mountains as well.

The skeletal material described herein has been received and catalogued as No. 121439 by the University of California Museum of Vertebrate Zoology in Berkeley.—RICHARD M. TULLAR, *Pierce Junior College, Woodland Hills, Calif. Received December 20, 1956.*

EVIDENCE OF THE FISHER IN CENTRAL ILLINOIS

A large quantity of animal remains was uncovered from a section of the Cahokia Site (Ramey Farm, Madison Co., Illinois) between mid-September, 1956, and January 1, 1957, by Gregory Perino, under the sponsorship of the Thomas Gilcrease Foundation, Tulsa, Oklahoma. The Cahokia Site was probably the largest Middle Mississippi site in North America (occupied approximately 1200 to 1550 A.D.) and included the area that is now East St. Louis as well as extensive regions to the north and south and along both banks of Cahokia Creek. Moorehead (Univ. of Illinois Bull., 26 (4), 1928) presented a rather complete description of the site, its history and cultural affiliations known at that time.

The bone remains, most of which were recovered from refuse pits and in scattered areas of midden debris in the village, were turned over to the author for identification. Typically, bones of the Virginia deer constituted the most abundant mammal remains, while those of squirrel (*Sciurus* spp.) were second, numerically. Other mammals, such as domestic dog, raccoon, beaver, cottontail, striped skunk, elk, muskrat and rice rat were also represented, as well as various species of fish and turtles. Bird bones were extremely numerous, those of ducks, geese and swans being most abundant.

Of special interest was the occurrence of a complete mandible and anterior section of the skull of an adult fisher, *Martes pennanti*, found in a refuse pit under the sloping fill of Mound No. 34. Although this mustelid formerly occurred as far south in the Allegheny Mountains as North Carolina in eastern United States, the southern limits of its range in Illinois during historic times included only the extreme northern section of the state. Kennicott (Trans. Ill. State Agr. Soc., 1 1855) stated that "The Fisher used frequently to be seen in the heavy timber along Lake Michigan." He later mentioned (Agr. Rept. for 1858, U.S. Patent Off., 1859) that "It has been found, within a few years, in Northern Illinois, and appears to be an inhabitant of the woods, alone." These appear to be sight records and specimens from Illinois are apparently non-existent.

It is quite possible that in prehistoric times the range of the fisher could have extended further south. Remains of the specimen recovered at Cahokia would tend to substantiate this since the extensive heavily wooded bottoms along the Mississippi River could have provided suitable habitat. Had the jaws or skull been worked or associated with a burial, indicating special significance, the animal might have been traded for or collected further north by the Indians, such a possibility being pointed out by Hoffmeister (Nat. Hist. Misc., Chicago Acad. Sci., No. 128, 1954) in case of worked jaws of the wolverine recovered from an Indian mound in Mason County, Illinois. Since the thickly timbered flood plain forests of the Mississippi River could afford a southern extension of habitat for the fisher, the remains of this animal found at Cahokia are quite possibly those of an animal taken in the vicinity. Guilday (Jour. Mamm., 37: 287, 1956) refers to a mandible section of a fisher uncovered in an archaic Indian site in West Virginia, thus indicative of its former, more southern distribution in that section of eastern United States. Additional faunal analysis work on animal remains recovered from Indian sites will aid greatly in establishing former ranges for many species.—PAUL W. PARMALEE, *Illinois State Museum, Springfield. Received January 18, 1957.*

A GEORGIA SPECIMEN OF THE MANATEE

On November 14, 1956, James M. Luker, a crane operator of the U.S. Army Corps of Engineers, brought me a box of bones from the north bank of the river, in Savannah Harbor, about 1 mile west of the center of the city. The box contained the major part of the skull of an adult manatee, *Trichechus manatus*, as well as the atlas, several vertebrae and a number of ribs. The bones were somewhat eroded, and had been buried in the sand and mud of the river bank at about high water mark. From my personal knowledge of this portion of the river bank, it is unlikely that the bones had been there more than 40 or 50 years, perhaps much less.

This appears to be the only actual specimen from this State, though there are a few sight records along the southern part of the Georgia coast (Jour. Mamm., 37: 288, 1956).—Ivan R. Tomkins, *1231 East 50th St., Savannah, Ga. Received January 24, 1957.*

CARNIVOROUS BEHAVIOR IN THE MEXICAN GROUND SQUIRREL

Perusal of the literature reveals no published account of carnivorous behavior in the Mexican ground squirrel, *Spermophilus mexicanus*, although such behavior has been recorded in other species of the genus (A. M. Johnson, Jour. Mamm., 3: 187, 1922).

On July 4, 1955, at 3:30 PM, while encamped one mile west of Parras, Coahuila, Mexico, Mr. DeLayne Hudspeth, Photographer for the University of Kansas Summer Field Party, informed me that he had just observed a ground squirrel near our campsite carrying a small animal. Hudspeth directed me to the area, where beneath a mesquite bush I observed a ground squirrel holding a small, live cottontail rabbit, *Sylvilagus* sp. It was approximately one-third as large as the ground squirrel. The ground squirrel, by means of its incisor teeth, was gnawing the rabbit in the scapular region. The noise that I made by stepping on a small twig caused the ground squirrel to drop the rabbit and leave. In approximately three minutes, nevertheless, the ground squirrel returned and picked up the rabbit by the neck. Thereupon I shot and obtained the ground squirrel, and picked up the rabbit still alive but bleeding from wounds in the region of the neck and shoulder. The right forefoot of the rabbit was missing. These wounds had seemingly been inflicted on the rabbit by the ground squirrel.

The ground squirrel (KU 67569), an adult male, referable to *S. m. parvidens*, weighed 198.8 grams, whereas the cottontail rabbit (KU 67566), a juvenile female, weighed 37 grams.—Robert L. Packard, *Museum of Natural History, Univ. of Kansas, Lawrence. Received February 9, 1957.*

LONGEVITY RECORDS FOR THE FOX SQUIRREL

A new longevity record for the fix squirrel, *Sciurus niger rufiventer*, is available in the records of the Rose Lake Wildlife Experiment Station near East Lansing, Michigan. One squirrel known to be 7½ years old was shot on the station on October 25, 1956, and another, at least 7½ years old, was shot there on October 23, 1952. These are the oldest squirrels in the 18-year record of the station. Regular live-trapping and tagging of game animals, exceptionally heavy hunting, and a bag check of all hunters on the station insure a high recovery of tagged animals.

The first squirrel, female No. 19209, was first trapped as a juvenile in a 10-acre oak-hickory woodlot on August 29, 1949. It was not handled again until shot, having moved over 1 mile from the place of first handling. A toe tag affixed for additional identification had been lost.

The second squirrel, a female No. 20499, was first trapped as an adult on August 28, 1946, in a swampy, oak-fringed woodlot. Before being shot six years later, it was retrapped 11 times, at least once each year. This record indicates that its entire life was spent within

an area of about 25 acres of similar habitat. Its weight ranged from 1 lb. 7 oz. to 1 lb. 15 oz. and averaged 1 lb. 10 oz. for the 13 times it was handled. A mild infestation of scabies on the hind legs and tail was noted in October, 1947, and in June, 1948.

It is interesting to note that a total of six toe tags and one ear tag was used on this squirrel. When last handled, five toes were missing from the hind feet. The ear tag (Style No. 1005, No. 3 fish tag, National Band and Tag Company, Newport, Ky.) was affixed at the time of first handling and was still in place when the animal was shot. The first toe tag, a monel metal "ring" described by M. E. Cooley (Jour. Wildl. Mgmt., 12: 213), was applied at the same time and was replaced as toes were lost. Despite the value of additional identification resulting from use of toe tags, they were discontinued in squirrel marking in 1955 pending investigation of the seriousness of occasional loss of toes.

Two additional squirrels have recently attained an age of at least 6½ years. Female No. 19547 was first trapped as an adult on March 1, 1950. It was retrapped on October 4, 1955. It had moved just over 1 mile from where first trapped. Male No. 20825 was trapped as an adult on June 8, 1951, and has been retrapped six times, last on September 19, 1956, within or near the same 10-acre oak woodlot. Its weight ranged from 1 lb. 9 oz. to 1 lb. 15 oz. and averaged 1 lb. 11 oz. for the seven handlings. This squirrel has lost one ear tag and three toe tags during its live-trapping history. Both squirrels have apparently survived the 1956 hunting season, and may equal or surpass the present longevity record of 7½ years.

These four fox squirrels, plus two reported by J. P. Linduska (Jour. Mamm., 28: 126–129) and H. C. Greene (Jour. Mamm. 31: 454–455) make a total of only six squirrels known to have surpassed an age of six years during the 18-year record of live-trapping at Rose Lake. —WILLIAM R. FOUCH, *Michigan Dept. of Conservation, Lansing. Received January 14, 1957.*

FAILURE OF MULE DEER TO WEAN OFFSPRING

Mule deer fawns, *Odocoileus hemionus*, are usually weaned when about five months old (Einarsen, THE DEER OF NORTH AMERICA, 1956, p. 382), and they then tend to remain with their mothers except while they are temporarily driven away for a period during the fawning season (Dasmann and Taber, Jour. Mamm., 37: 143–164, 1956).

On one occasion, however, a yearling mule deer and a fawn were observed being nursed simultaneously by an older doe. The incident occurred on October 8, 1954, on a study area located in the chaparral vegetation near Prescott, Arizona. The fawn appeared to have been born about September 1, although the peak of fawning in that region was about August 1 (Hanson and McCulloch, Trans. N. Amer. Wildl. Conf., 20: 568–588, 1955). The behavior of the animals indicated that the yearling was accepted by the mother on nearly the same basis as the fawn.

A somewhat similar case was seen on June 10, 1954, in the Juniper Mountains about 40 miles northwest of the previously mentioned area. During the short time that a group of deer was observed, also in a chaparral community, two immature animals nursed one doe sporadically, but they were not repulsed. Although the immature deer were fairly small, they must have been at least nine months old. The udder of the doe seemed to have little or no milk. However, if the immature deer had continued with this behavior for another six weeks, their efforts should have been better rewarded, and competition with the new offspring might again have resulted.

Numerous persons including the writer have observed that the adult doe takes the initiative in ending family relationships, particularly nursing. Obviously, failure of the mother to break the nursing bond could endanger her life and, later, that of the new offspring.

Acknowledgment is made to Drs. Thomas G. Scott, Ralph E. Yeatter and Carl O. Mohr, and to Mrs. Frances Robbins, all of the Illinois Natural History Survey, for editorial assistance.
—WILLIAM R. HANSON, *Illinois Natural History Survey, Urbana. Received January 29, 1957.*

UNUSUAL DENTITION IN MULE DEER

Cowan (Canad. Jour. Res., *D*, 24: 71–103) states that "variations in numbers of teeth in the genus *Odocoileus* are rare." He further reports but one instance of supernumerary incisors in *Odocoileus hemionus* and quotes two cases of canines encountered by Nordquist (Calif. Fish and Game, 27(1): 39–40). Because of this apparent rarity of variations in number of teeth the writer is reporting on four cases of fewer teeth than normal and four cases of more than normal which he has encountered among Rocky Mountain mule deer, *O. h. hemionus*, of Utah and eastern Nevada.

Fewer than normal deciduous or permanent teeth.—Case 1 involved a 28-month-old doe with all permanent premolars functional except the first one (P_3) of the left mandible, where a tiny milk tooth 2 mm. in height and in diameter was still retained. Removal of the underlying bone revealed no corresponding permanent tooth. Permanent teeth of mule deer are normally formed several months in advance of actual eruption and in this instance the permanent tooth had not yet formed, even though the remaining premolars were all permanent and had been functional for several months.

Case 2 concerned a doe estimated to be a 6-year-old that had but six permanent incisiform teeth. The "corner incisors" or canines were missing. Bone removal revealed no impacted canines nor evidence that there had ever been any.

A similar condition was noted in Case 3 which concerned a female fawn killed March 18, when about 9 months of age. The fawn had six milk incisors with the canines missing. As in Case 2, there was no evidence that the canines had been broken off or remained embedded in the bone.

Case 4 was a doe of about 21 months that still retained its first or middle pair of milk incisors while the remaining incisiform teeth were all permanent. No trace of the first pair of permanent incisors could be found embedded in the mandible.

Cases of supernumerary teeth.—Case 1 was a 3-year-old buck having a single canine in the right maxilla. Upper canines are apparently much more prevalent in white-tailed deer, for Severinghaus found 23 in 18,000 (Van Gelder and Hoffmeister, Jour. Wildl. Mgt., 17: 100—editor's note) for an incidence of 0.13 per cent compared to 2 in 4,000 mule deer or an incidence of 0.05 per cent as observed by Nordquist (*ibid.*).

Case 2 involved a 2-week-old fawn that had an extra milk incisor which had erupted posteriorly but adjacent to the second and third incisors of the right mandible. No companion to it could be found in the bone of the left mandible.

In Case 3, a pair of supernumerary permanent incisors was found in a buck killed by a hunter in October, 1956, in central Utah. Location and shape of the teeth would indicate that they were an extra pair of the first or middle pair of permanent incisors. The left member of the supernumerary incisors had erupted between I_1 and I_2 of the original set on the left side and, because of the crowding, was in a tilted position with its transverse axis in a nearly vertical position. The right member was properly oriented except for being located posteriorly to original I_1, of the right mandible. The buck was estimated from wear of the molariform teeth, to be about a 5-year-old. Wear on the original set of incisors conformed to this age but the supernumerary pair showed little wear and had probably errupted only a few months previously.

Fowle and Passmore (Jour. Mamm., 29: 301) reported a supernumerary incisor in an adult white-tailed buck and the case of an extra inciscor reported by Cowan has already been mentioned.

Case 4 was a 3-year-old doe from the Duck Creek area of eastern Nevada that had an extra permanent premolar in the left mandible. The tooth, which was similar in size and form to the second permanent premolar (P_2) in the tooth row, was wedged partially between normal P_2 and P_3 but had been largely crowded from the tooth row to the buccal side. None of the premolars was a retained milk tooth.

Several instances of anomalies in position of the incisiform teeth have been noted, the most common being the rotation of a tooth 45 to 180° from its normal position. One case was noted where, perhaps due to crowding, the third permanent incisor of the left mandible had erupted posteriorly to the second.—W. Leslie Robinette, *U.S. Fish and Wildlife Service, Salt Lake City, Utah. Received January 8, 1957.*

ON THE RELATIVE EFFICIENCY OF TWO KINDS OF TRAPS

The most successful method of estimating small mammal population densities is some sort of trapping program. For studies over large areas where transportation difficulties arise, snap traps are usually employed because they are comparatively easy to pack and carry. All results of such programs depend on all animals being equally susceptible to the traps.

As a part of a long-term study of fluctuations of small mammal populations, one-acre quadrats had been established in 1954 at several widely separated points in Alaska. In previous years they had been trapped for three nights with Schuyler Size 3 "Mouse Killers" (J. R. Schuyler and Co., Bloomsburg, Penn.). Each area was gridded and equipped with permanent wire markers so that 100 traps could be equally spaced on it. All traps were equipped with a length of stout cord 0.8 meters long with a loop which was slipped over the wire marker. Thus the traps, in each succeeding year, have been placed within the same 2 square meters. This method has been used in order to minimize the effects of different amounts of trapping experience by different operators.

During the summer of 1956, instead of 100 Schuyler traps being used on each quadrat, 50 Museum Special traps (Animal Trap Co. of America, Lititz, Penn.) and 50 Schuyler traps were used at the same time, one of each kind at alternate markers. Bait was a standard mixture of rolled oats, peanut butter, chopped raisins and bacon grease. Approximately the same amount of bait was used with each trap. Thus each type of trap was given as nearly equal "presentation" to the animals as was possible.

Table 1.—*Captures by two types of traps on four quadrats, 1956*

Species	Museum Special	Schuyler
Clethrionomys rutilus	10	6
Microtus miurus	10	5
Microtus oeconomus	0	14

Table 1 shows the results of 1200 trap-nights on four of the quadrats where animals were taken during the summer of 1956. The two quadrats that produced *Microtus oeconomus* were situated one on the Baldwin Peninsula and one at Northeast Cape, St. Lawrence Island, in lowland grass-sedge tundra. The quadrat that produced *Microtus miurus* and some of the *Clethrionomys rutilus* was situated near Old John Lake in northeast Alaska in scattered spruce–dwarf birch–alder "forest-tundra." The quadrat that produced the bulk of the *Clethrionomys rutilus* was situated near Fairbanks in virgin white spruce forest with a deep mossy floor cover. Testing these ratios by chi square shows that the observed discrepancies in the ratios of animals caught would arise by chance more than 5 times in 100 in the cases of *Clethrionomys rutilus* and *Microtus miurus*, but far less often than that in the case of *Microtus oeconomus*. Thus we may state that *Clethrionomys rutilus* and *Microtus miurus* appear to be equally susceptible to being caught in Museum Special or in Schuyler traps while *Microtus oeconomus* appears to be far more suspectible to being caught in Schuyler traps.

We are grateful to the Arctic Aeromedical Laboratory, Ladd AFB, Fairbanks, Alaska, for the support which made this study possible.—William O. Pruitt, Jr. and Charles V. Lucier, *Box 282, College, Alaska.* *Received January 8, 1957.*

DACRON AS A FILLING MATERIAL FOR SMALL MAMMAL SKINS

The difficulty of obtaining good, fluffy, long-staple cotton for filling study skins of small mammals has led to the use of synthetic fiber for this purpose by the authors. Our experiences with Du Pont Dacron batting have encouraged us to write this note. This batting has been tested by the preparation of a number of study skins varying in size from bats to small carnivores, and has proved superior to even the better grades of cotton batting. Its high resiliency produces a soft specimen of normal contours which will spring back into shape after being distorted. Since it has a long fiber length, this material is also suitable for wrapping legs and tail wires. After one becomes accustomed to the characteristics of Dacron batting, exceptionally uniform specimens may be made up with less effort, we believe, than that required with cotton batting.

Dacron would appear to be at least as inert chemically as cotton. Mauersberger (American Handbook of Synthetic Textiles, 1952: 341) states that "this polyester fiber has excellent resistance to degradation by bleaches and common solvents and its general resistance to chemicals is good." Its absorption of water is low. This may be a deterrent to its use in climates where specimens tend to dry slowly. We have not had the opportunity of testing Dacron in any but the dry southwestern climate, where it has proved entirely satisfactory. —KEITH E. JUSTICE AND WILLIAM J. SCHALDACH, *Dept. of Zoology, Univ. of Arizona, Tucson. Received January 22, 1957.*

PERSONAL NOTICES

This space is available to members of the Society for brief notices of interest to mammalogists. Copy should be sent to the editor by the 10th of the month preceding publication. Rates for single insertion are 25 cents per line or portion thereof. Bills will be rendered following publication.

FOR SALE—*Japanese "Mist" Bat Nets.* Send for price list. W. B. Davis, 254 F.E., College Station, Texas.

FOR SALE—*Live desert rodents.* Send for information and price list. Keith E. Justice, 44 W. Rillito St., Tucson, Arizona.

WANTED—*Preserved specimens,* just hatched or born, full term; all species; identified; maximum 12 hours. David Wetherbee, Hampton, Connecticut.

GLEANINGS FROM THE FIELD

Our liaison officer with Russian mammalogists, E. W. Pfeiffer, is now affiliated with the Department of Anatomy, University of North Dakota, Grand Forks; Karl F. Koopman may now be reached at The Academy of Natural Sciences of Philadelphia; from Stoney Rapids, Saskatchewan, comes word that William O. Pruitt, Jr., has "come to roost for three or four months in my wanderings over northern Canada following the caribou." We learn that Dale J. Osborn recently became Head of the Department of Biology, Robert College, Istanbul, Turkey. Please send in *your* news to the editor.

1958 ANNUAL MEETING

Plan now to participate in the 38th Annual Meeting of the Society to be held this June at Tucson, Arizona. See further details in this issue, page 173.

REVIEWS

Blair, W. Frank, Albert P. Blair, Pierce Brodkorb, Fred R. Cagle and George A. Moore. VERTEBRATES OF THE UNITED STATES. McGraw-Hill Book Company, Inc., New York. Pp. x + 819, illus. August 29, 1957. Price, $12.00.

Years ago, Jordan's MANUAL OF THE VERTEBRATE ANIMALS OF THE NORTHEASTERN UNITED STATES served as a bible to students of vertebrate biology; its 13 editions attest to its usefulness, although the last printing (1929) was woefully out-of-date. Pratt's MANUAL OF THE LAND AND FRESH WATER VERTEBRATE ANIMALS later served a similar purpose, but the last revision (1935) has been unavailable since the late forties. This worthy successor comes at a particularly opportune time, when interest in the field is at a higher level than ever before. VERTEBRATES OF THE UNITED STATES should more than adequately meet the needs of students and others for a taxonomic guide.

Unlike its forerunners, this volume covers the entire vertebrate fauna of the whole country. All species occurring in the continental United States and its adjacent waters (excepting marine fishes and turtles) are considered; subspecies are not treated. Each class is dealt with by a qualified specialist and teacher: fishes by Moore (178 pp.), amphibians by A. P. Blair (59 pp.), reptiles by Cagle (84 pp.), birds by Brodkorb (353 pp.) and mammals by W. F. Blair (158 pp.). The senior author contributes a substantial Introduction (27 pp.) with a consideration of vertebrate history as regards paired appendages, jaws, terrestrial habits and the development of homoiothermy; the various organ systems and their functions; and detailed, up-to-date ideas on classification, nomenclature and distribution. In the section on birds many students will be delighted to find a treatment of such ordinal and family characters as pterylography, palatal structure, position of coracoids, plantar tendons, convolutions of the small intestine, and leg and syringeal musculature. An extensive Glossary and detailed Index complete the volume.

An effort was made to achieve unanimity in the five major parts of the book and they do follow one general plan. For each group there is a discussion of its morphological traits, geological history, classification and characters for identification. Simple dichotomous keys to all subordinate categories are provided. Each taxon is characterized as it exists on a world-wide basis, and its geologic and geographic ranges are indicated. Detailed tables for each group list all known orders, with a census of families (genera and species in certain cases); living and extinct groups are designated. It is disconcerting to find that among fishes and mammals a dagger (†) indicates fossil forms, among birds it indicates extralimital groups, while among amphibians and reptiles it is not employed. Treatment of references also varies widely, from the 141 titles pertaining to fishes to none at all for birds. The 71 selected references on mammals seem unnecessarily skimpy for such an inclusive work; 13 are general, 10 regional in nature; the rodents rate 27 titles, the insectivores only 3. Included are recent works as well as some older classics.

The section on mammals is well organized and should serve admirably for taxonomic purposes. Recent techniques and contributions (as on *Mustela* and *Reithrodontomys*) have been incorporated where appropriate. Ranges of measurements, dental formulae, color pattern, character of the pelage, nature of planter pads, number and position of mammae, skeletal features and other characters are listed. Of the standard external measurements, those of ear length are generally omitted as being unavailable or unreliable in many specimens. The structure of the baculum is utilized in *Dipodomys, Neotoma, Perognathus* and *Peromyscus*. For several forms (*Citellus, Erethizon, Zapus*) oblique views of the skull are figured; these illustrate certain features much better than the customary straight-on lateral views. The figures reproduced (p. 769, from Seton) to typify the antlers of *Odocoileus* seem a poor choice inasmuch as they depict atypical specimens. Both black and grizzly bears are

included under *Ursus*, and *Citellus* is retained for the 19 species of ground squirrels. The genera *Microtus*, *Odocoileus* and *Vulpes*, mercifully, have been left undisturbed. Common names, wherever established, are given for all categories. Sooner or later some student, reading (p. 620) that the "graviportal limb skeleton, large hypsodont and lophodont molars . . . are a few of the peculiarities" of proboscideans, will be frustrated to find that none of these technical terms are included in either Glossary or Index.

This reviewer is irritated by several features, but for the most part these are minor and do not affect the usefulness of the book. Illustrations are plentiful and well-chosen; the line cuts are of generally good quality, but many of the halftones leave something to be desired. Side headings of the same degree, not set off by spacing, serve for orders, families and genera alike; this almost certainly will lead to confusion. Economy of space undoubtedly dictated this style, as it did the consistent use of figures. However, beginning a sentence (p. 18) with "2 populations may stand . . ." or (p. 619) with "6 of the 8 living families . . ." seems to be carrying economy to extremes.

In view of the magnitude of the job, amazingly few errors have crept into the pages. The book contains a wealth of detail never before brought together in one place, and it is sure to be a boon to students, field collectors, taxonomists and vertebrate biologists generally. The authors deserve the acclaim of their colleagues for the time and effort that went into the undertaking. But this is primarily a book on the identification of species; only rarely is mention made of foods, habitat, breeding habits, or behavior in general. As a taxonomic guide it is splendid, but it will scarcely justify the publisher's grandiose claim, on the jacket, that "it will serve as a textbook for courses in . . . ecology and natural history." The price, pegged where it is in the absence of competition, will tend to place the volume in the reference room rather than on the student's worktable where it belongs.—RICHARD H. MANVILLE.

Hoffmeister, D. F. and C. O. Mohr. FIELDBOOK OF ILLINOIS MAMMALS. Manual 4, Natural History Survey Division, Urbana. xi + 233 pp., 119 figs. (74 halftones), 1 color pl., 19 maps. June, 1957. Price, $1.75.

The Illinois Natural History Survey is charged by state statute with publishing "from time to time, reports covering the entire field of zoology and botany of the State." This manual, begun over a decade ago by Dr. Mohr and subsequently completed by Dr. Hoffmeister with the collaboration of Dr. Mohr, is a commendable response to that charge.

Designed primarily for the amateur naturalist, the manual contains rather brief but thoughtful sections on mammal habitats, types of distribution, how to study mammals, recognition of mammal signs, and the use of taxonomic keys. The synopsis covers 59 species known to occur in the state; others such as the bison, pronghorn, elk and timber wolf which have been recorded in Illinois but which have since disappeared; species such as the hispid cotton rat (*Sigmodon hispidus*) and the short-tailed weasel (*Mustela erminea*) which have not been recorded but are likely to occur in Illinois; and prehistoric mammals. There is a brief description of the characteristics of the Class Mammalia and a key to the orders. For each order there are two keys to species, one based on external characters and one on skull and tooth characters.

Each species is described according to its external morphology, pelage, body measurements and weight, skull characters and dental formula. Facts about their life histories include a dicussion of general habits, breeding activity, litter size, development and care of the young, food habits, seasonal activity and economic importance. The signs of each species, including descriptions of their tracks, homes, food caches and droppings are given with suggestions for recognizing evidence of their activities. The species' distribution in Illinois and its range in the United States are both given. Distributions are illustrated for those species with restricted ranges in Illinois, although a detailed map of the state distribution,

rather than a map of its range in the United States, would perhaps be more useful in these cases. Of the 59 species of mammals known to occur in Illinois, 45 are represented by excellent photographs of the adults. The subspecies that are known to occur in Illinois are listed but not described.

This manual has been thoughtfully prepared with careful consideration for the interest and needs of the amateur and beginning student of mammalogy. A particularly useful feature is an introductory section on mammal habits and signs. With the aid of a key to mammal tracks and several excellent photographs and line drawings of mammal tracks and homes, the reader is told how to recognize many mammals by the evidence of their activities. Since many species are seldom seen outside study collections, this information will certainly be of value to many users of the manual. Of further aid to the amateur or beginning student are a glossary of 125 key terms; a bibliography of literature on Illinois mammals, mammals of the United States, and species that occur in states near Illinois; labeled illustrations of different views of a mammal skull; and instructions for collecting and preserving specimens. —RICHARD S. MILLER.

Moore, Joseph Curtis. THE NATURAL HISTORY OF THE FOX SQUIRREL, SCIURUS NIGER SHERMANI. Bull. Amer. Mus. Nat. Hist., vol. 113, art. 1, pp. 1–72, 7 figs., 3 pl. August 26, 1957. Price, $1.50.

The fox squirrel, because of its abundance, ease of observation, importance as a game animal and general biological significance, has been a favorite subject of many investigators. No detailed study, however, has been made of the ecology of this large race of the southeastern coastal plain and the reader will learn that in several particulars this Florida population differs markedly from its counterparts elsewhere. This is a shy, rare creature of the northern Florida sand hills. Its foods are largely pine seeds and acorns; its chief enemies are the bald eagle, the red-tailed hawk and, particularly, man and his dog. Its original home, presumably, was in the open stands of large longleaf pines; but the increasing human population, with the resulting elimination (by axe, saw and fire) of much of the natural wilderness and its replacement by turkey-oak forests, forced the squirrel to adapt to changed conditions. This it has done with moderate success and therein lies the significance of this highly readable account.

This study is based largely on observations at the Conservation Reserve of the University of Florida at Welaka, Putnam County, in 1946 and 1947. Aside from observations on wild animals, 506 nests were examined *in situ*, 24 specimens were collected for parasites and other data, and nine young (representing five broods) were reared in captivity. Subjected to special scrutiny was the 52.3-acre North Five Area. Here, during July and August, were 65 nests and a population (exclusive of nestlings) of eight squirrels; this represented a density of one breeding female per 13 acres, or of one animal per 6.5 acres, probably near the optimum for this community but low in comparison to areas in Ohio and Michigan. The excessive number of outside nests served as refuges and, with the shifting of broods from one nest to another, probably helped to reduce infestation by the squirrel flea. The underground burrows of gopher tortoises were used as refuges, as well as the hollows in old pine stumps (two of which led to underground nesting chambers)—strange indeed for a tree squirrel. A peculiar device for hiding from man consisted of climbing to the extreme top of a pine tree so that the plume-like growing tip bent down and obscured the squirrel from below.

Five types of "outside" or "leaf" nests are described. In summer, these may be constructed of the leafy twigs of turkey oak, good protection against rain; in winter, pinestraw and dried grass or Spanish moss furnish better protection against cold. The squirrels' tails are also protective in function, warding off mosquitoes and serving variously as umbrellas, blankets or sunshades. Caching of winter food stores is not the common practice in this area.

Adults appear to molt but once a year, at almost any time but more often in summer. The voice includes a high-pitched cry (of distress?) by the young, a series of churring or chucking grunts, and the familiar barks, similar to those of the gray squirrel but with the two component sounds reversed. Limited territoriality is suggested and in captive broods dominance by the males was noted.

The author's distinctive style is a highly effective one. Describing drinking by a captive specimen, he writes: "I crouched with my head to the ground and eyes within 8 inches of his mouth. . . . He did not lap the water, or even expose his tongue, but sucked the water up as does a horse." The captive individuals are designated by Greek letters. Thus we read that "Eta, Theta, and Lambda had no opportunity to cache food until they were 99 days old, . . . when they responded abundantly to their first chance. When Omicron cached the 16 live-oak acorns . . . his technique differed from that described for Gamma." The author takes pains to point out shortcomings in the use of Standard Time for recording activity; instead, he uses sunrise (or sunset) plus or minus so many hours and minutes. "On February 4, 1947, at sunrise plus 24 minutes a full-grown fox squirrel left the nest when the writer was halfway up to it." More general use of this system for recording activity of diurnal animals would probably be profitable.

This bulletin may well serve as a model for life-history studies of local populations. The author has reviewed and evaluated the pertinent literature (67 titles cited) with discernment, has painstakingly and efficiently gathered his data from observation and experiment, and has presented his findings in a delightfully entertaining and lucid style. Such conclusions as seem justified are spelled out with care. The illustrations, all from the author's facile pen, add to the presentation and to the general attractiveness of the work.—RICHARD H. MANVILLE.

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COMMENTS AND NEWS

THIRTY-EIGHTH ANNUAL MEETING

The thirty-eighth annual meeting of the American Society of Mammalogists will be held in the Biological Science Building at the University of Arizona, Tucson, Arizona, on June 16–18, 1958. Registration and papers will be in this building. The Directors' meeting will be at 8:00 PM, on June 15. Open sessions will begin on Monday morning, June 16. A call for papers will be distributed to all members by the Secretary-Treasurer in the spring but, since only approximately 50 papers will be allowed on the program this year, the title, as well as an estimate of the amount of time needed, should be sent to the Secretary-Treasurer well in advance of the May 1 deadline. If a selection of papers must be made, preference will be given to those dealing with the results of independent research. Papers to be considered for the honorarium must be submitted by April 1 and should be submitted well in advance of that date. The Chairman of the Local Committee will be E. Lendell Cockrum.

Tucson is well known as a tourist mecca. It has a large number of hotels, motels, guest ranches and resorts in and around the city. Off-season rates will be in effect during the time of the meetings. Rates range from $3.00 per night up. A list of accommodations may be obtained from the Chamber of Commerce, P.O. Box 991, Tucson, and reservations for these may be made directly with the Chamber of Commerce, if desired. Housing for single persons will be available on the campus in air-conditioned dormitories at the rate of $2.00 per night, with two persons to a room. Reservations for these spaces must be made on or before June 1 by writing to Robert B. Chiasson, Department of Zoology, University of Arizona, Tucson.

Tucson, Arizona, is served by the Southern Pacific railroad, Greyhound and Trailways bus lines, and American, Trans World and Frontier airlines.

RESOLUTIONS

Members having resolutions intended for action by the Society at its next annual meeting are urged to submit them to the Resolutions Committee at the earliest opportunity. The committee is anxious to submit the proposals to the members prior to the meeting but can do so only if they receive such proposals at an early date. May 1, 1958, has been set as a deadline. Proposed resolutions should be sent to the Committee Chairman, Dr. Keith R. Kelson, National Science Foundation, Washington 25, D. C.

HONORARIA

Two honoraria are available each year for young mammalogists who have not obtained the Ph.D. degree. These honoraria carry a stipend of $100.00 each to help defray the expenses of travel to the annual meetings for the presentation of the paper. In 1958 the meetings will be held in Tucson, Arizona, about the middle of June. Entries should be submitted to Dr. Stephen D. Durrant, Department of Zoology, University of Utah, Salt Lake City, Utah, before April 1, 1958.

PROPOSED AMENDMENT OF BYLAWS

The Board of Directors proposes to submit the following changes in the Bylaws to the membership of the Society at the annual meeting in June for action. These involve raising annual dues from $4.00 to $5.00 and life membership fees from $100.00 to $125.00.

Amend Sections 1 and 2 of Article VIII to read as follows:

SEC. 1. Annual dues for members shall be five dollars payable in advance.

SEC. 2. Any member upon payment of one hundred twenty-five dollars at one time or in four consecutive, equal annual payments shall be entitled to life membership, and shall be exempt from annual dues.

These changes appear to be necessary to put the Society on a sound financial basis. In spite of an income of approximately $4,000 from investments to add to the income from annual dues and subscriptions, expenses are exceeding income.

If the amendments are approved, it is anticipated that the increase in life membership fees to $125.00 will not apply to those members who have made the initial payment on this class of membership at the current rate of $100.00 prior to the effective date of the increase. Those of you who desire to take advantage of the current low life membership fee and avoid the anticipated increase should contact Dr. Bryan P. Glass, Secretary-Treasurer, Department of Zoology, Oklahoma State University, Stillwater.

NEW JOURNAL

The Division of Biological Sciences and the Press of the University of Chicago announce the publication of PERSPECTIVES IN BIOLOGY AND MEDICINE, a new quarterly journal dedicated to a multidisciplined approach to the problems of biology and medicine. The first issue appeared in November, 1957. PERSPECTIVES will present new hypotheses and concepts representing informed thinking; interpretive, selective essays which take stock of the implications of recent and current research and indicate strategy for the future; and, because perspective and inspiration can also be gained by looking to the past, reviews by great men in science and medicine of their formative years and their philosophy of research.

COLLOQUIUM ON UNGULATES

About sixty zoologists from Belgium, Denmark, France, Germany, Great Britain, Holland, Italy, Russia, Switzerland and the United States attended a colloquium in Paris on the Systematics and Biology of the Ungulates from October 23–26, 1957, arranged by the Comité de Direction et d'Administration of the journal *Mammalia* and the (Benelux) Société pour l'Etude et la Protection des Mammifères. Some thirty papers on such aspects of the subject as classification, conservation, blood groups, placental structure, behavior, and the biology of particular species were presented. The texts of these papers, together with some others not presented at the colloquium, will be published in full in *Mammalia*.

1957 CONSERVATION DIRECTORY

This annual publication of the National Wildlife Federation, enlarged this year to 102 pages, contains listings of officers and personnel of public and private conservation agencies in the United States, Canada, Latin America and the Philippines. Copies may be ordered at 50 cents each (40 cents each for more than 25) from Directory, National Wildlife Federation, 232 Carroll Street, N.W., Washington 12, D.C.

COLLOQUIUM ON ZOOLOGICAL NOMENCLATURE

A communication from Francis Hemming, Secretary to the International Trust for Zoological Nomenclature, announces a Colloquium on Zoological Nomenclature to be held in London in connection with the 15th International Congress of Zoology. The Colloquium, by examination of the draft of the revised Code and discussion of the questions involved, will assist the Congress in carrying through the detailed survey of the proposed text of the International Code of Zoological Nomenclature, as amended by the Paris and Copenhagen Congresses in 1948 and 1953, respectively, which will be required before it can give its approval to that text and issue directions for its promulgation.

The Colloquium will open on July 9, 1958, one week prior to the opening of the London Congress. It is hoped that it will relieve the Congress of the bulk of the work of scrutinizing the draft of the revised Code and will submit recommendations as to the text to be adopted. Invitations to the Colloquium have been issued to a large number of zoologists known to be interested in zoological nomenclature; further invitation will be issued by the Trust to any member of the Congress who expresses a desire to take part in its discussions but who has not as yet received a separate invitation.

PROJECT ON GENERA OF MAMMALS

Ernest P. Walker is seeking black-and-white pictures of live wild mammals, preferably with little or no vegetation or other background to obscure or detract from the subject. The pictures are for publication in a research and writing project entitled "Genera of Recent Mammals of the World," financed by the U.S. National Institutes of Health. This project is the first of its kind to attempt to bring together pictures of at least one representative of each genus of Recent mammals and basic information about it. It will be written in clearly understandable English and published at or near cost. Persons who have pictures of mammals from any portion of the world, particularly South America, Africa and the southern Asiatic region, are invited to communicate with Mr. Walker at 3016 Tilden St., N.W., Washington 8, D.C., but not to send pictures until they have first been in touch with him. Moderate prices are paid for black-and-white pictures of the type that he can use in the project, and exclusive use is not required.

REPORT AVAILABLE

The International Union for Conservation of Nature and Natural Resources held its Sixth Technical Meeting at Edinburgh, Scotland, in June, 1956, with participants present from 37 different countries. The proceedings and papers of this meeting, including texts or summaries of over eighty papers, comprise an impressive volume of 265 pages, illustrated. Copies are available at $3.75 (paper) from The Nature Conservancy, 19 Belgrave Square, London S.W. 1, England.

DEATH REPORTED

Eleanor Jean Leland, November 22, 1957

SUGGESTIONS TO AUTHORS

The *Journal of Mammalogy* publishes original papers with significant new material on any phase of the science of mammalogy. While authors need not necessarily be members of the society, it is suggested that those doing serious work in this field consider carefully the desirability of affiliating with the American Society of Mammalogists.

Papers are generally published in order of receipt with some exceptions at the discretion of the editor. Papers over 20 printed pages in length are rarely published because of cost and space limitations. When subsidized, however, such papers may occasionally be published. Photographic and tabular matter, likewise, will be accepted only when necessary to the exposition of the paper and when the data or point presented are not repeated in the text.

A neat, carefully prepared manuscript is assured more favorable consideration by the editors. It also expedites processing and is more likely to appear in print as the author intended it. Toward this end, the following suggestions are offered as a guide:

All manuscripts should be typewritten on one side only of a good quality white bond paper, preferably 8½ × 11″ in size. All material—*including titles, by-lines, headings, tables, extracts, references and legends*—should be double-spaced. Carbon copies will not be accepted, nor will originals on onionskin or highly glazed paper. Pages should be numbered consecutively in the upper right corner. Tables (with captions) and the legends for figures and plates should be typed on separate pages following the text. All margins should be at least 1½″ wide. Do not mark for typography, except to indicate *italics* by underscoring.

Titles should be brief as an aid to bibliography. Usually less than ten words will suffice. Avoid citing scientific names in the title but incorporate them early in the text.

Acknowledgments and reference to sponsorship and contract number are included in the text. Avoid footnotes hung from the text. Note author's affiliation at the end of the article. This should be concise—it is intended to furnish his current address, not his biography.

References, when less than six in number, should be inserted in parentheses at appropriate spots in the text; they should include author, publication, volume, pagination and year, but not title unless a book. More extensive references, arranged alphabetically by author and with title included, are grouped under "Literature Cited." In general, our bibliographic style follows the suggestions made in the A.I.B.S. Bul., 2 (2): 21–23, 1952.

Standard abbreviations are used freely, particularly in tables and with units of measure, *e.g.*, 5.7 mm., 12 cc., 23 lb., 5 hr., 35 mph, 20°C.

Tables should be typed on separate terminal pages and should be arranged as simply as possible to fit Journal page size. It is not always necessary to present all data at hand; the author should exercise some judgment as to what data are essential. Include the units of measure employed. Do not insert rules except in box heads, and then only lightly in pencil.

Figures include black-and-white drawings and graphs reproduced as line cuts. Originals should be submitted. Some reduction is desirable, but a drawing need not be more than twice the size of the intended cut. If a scale is included, anticipate its reduction in size. Labels also must be planned to be easily legible when reduced. All lines must be solid black, not gray. Graphs may be made on paper with pale blue lines which will not reproduce.

Plates are photographs reproduced as halftones. The originals must be sharp, with high contrast, and printed on glossy paper; they should be submitted unmounted. A size of 4 × 5″ is ordinarily most convenient. Each should be identified by a light pencil notation on the back. Cropping to remove non-essential portions is often desirable.

A summary, brief and informative, is advisable at the end of major papers.

Authors are urged to consult recent issues of the Journal for examples of styling. *A Manual of Style,* Univ. Chicago Press, is a standard guide. The Government Printing Office *Style Manual* is especially helpful on capitalization. The final authority for spelling is Webster's *New International Dictionary,* unabridged. Webster's *New Collegiate Dictionary* is adequate for most purposes; it contains a useful appendix with rules for punctuation, capitalization, hyphenation, preparation of copy, and proofreaders' marks. Fowler's *Modern English Usage* is a sound and entertaining reference on grammar and writing in general.

Proof should be read word for word immediately upon receipt and returned promptly, with manuscript, *to the editor.* Errors should be corrected in the margin, but galleys are not the place for widespread corrections by the author. Essential changes or additions are best added at the end of a paragraph, or inserted as a new paragraph. Extensive changes from the original copy will be charged to the author. Cuts should be identified by number, the desired placement of tables and figures indicated in the margin and, where it is not evident, each cut should be labeled TOP on one side.

Reprints may be ordered directly *from the printer* when galleys are checked. An order form is supplied with the proof. One hundred reprints, without covers, are furnished gratis to authors of major articles, provided that at least 100 additional reprints are also ordered.

Abstracts of major papers should be prepared and returned with corrected proof.